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Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: Physics to fish and coasts to ocean

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ABSTRACT

It has long been recognised that there are strong interactions and feedbacks between climate, upper ocean biogeochemistry and marine food webs, and also that food web structure and phytoplankton community distribution are important determinants of variability in carbon production and export from the euphotic zone. Numerical models provide a vital tool to explore these interactions, given their capability to investigate multiple connected components of the system and the sensitivity to multiple drivers, including potential future conditions. A major driver for ecosystem model development is the demand for quantitative tools to support ecosystem-based management initiatives. The purpose of this paper is to review approaches to the modelling of marine ecosystems with a focus on the North Atlantic Ocean and its adjacent shelf seas, and to highlight the challenges they face and suggest ways forward. We consider the state of the art in simulating oceans and shelf sea physics, planktonic and higher trophic level ecosystems, and look towards building an integrative approach with these existing tools. We note how the different approaches have evolved historically and that many of the previous obstacles to harmonisation may no longer be present. We illustrate this with examples from the on-going and planned modelling effort in the Integrative Modelling Work Package of the EURO-BASIN programme.

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Introduction

The North Atlantic Ocean and its contiguous shelf seas provide a diverse range of goods (e.g. food, renewable energy, transport) and services (e.g. carbon and nutrient cycling and biodiversity) to mankind. However, global climate change will lead to substantial changes in the physical conditions of the basin (e.g. circulation, stratification, temperature and light climate). At the same time, combinations of direct anthropogenic drivers (e.g. fishing and eutrophication) impact at both an organismal and population level, thereby influencing the biogeochemical cycles of carbon and nutrients on a regional and basin wide scale. The coupling between the climate, marine ecosystems and the human impacts on these

ecosystems is a key facet of the Earth System, of which our understanding is only beginning to scratch the surface. This coupling relates to two overarching scientific issues of immense societal concern:

- the role of the oceans in mitigating the effects of anthropogenic CO₂ emissions,
- the impacts of climate (change and variability) and fishing pressure on ecosystem structure and function, and the consequences for biodiversity and fisheries production.

BASIN (Wiebe et al., 2009) is a joint EU/North American research initiative with the goal of elucidating the mechanisms underlying observed changes in North Atlantic ecosystems and their services, and EURO-BASIN is a programme to implement this, funded under the European Commission's 7th Framework

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Programme. Much can be learned on these issues through an extensive observational and experimental effort, however, a crucial challenge for BASIN is to develop the predictive capability necessary to understand the space and time variation of broadly distributed and dominant members of the North Atlantic plankton and fish communities, the relevant biogeochemical processes, as well as feedbacks between and within these components and climate. It is only through the development and application of integrative modelling that these questions can be explored together and under possible future conditions, potentially far removed from any conditions in the observational base. In this paper, we explore the fundamental challenges of an integrative approach to modelling the marine ecosystem in the North Atlantic and its adjacent shelf seas, with a focus on these overarching issues. To illustrate this, we draw on examples from the Integrative Modelling Work Package in the EURO-BASIN programme, where state of the art models of physical, lower and higher trophic level processes are deployed. In the remainder of this introduction we set the scene by considering how these two overarching issues give rise to key science objectives in this region.

While the open-ocean (Sanders et al., this volume) and shelf seas (e.g. Chen and Borges, 2009) biological carbon pumps are well established, the dynamics of these processes and their vulnerability to future change are far from certain. This is particularly the case in the context of changing marine management strategies and physical, ecosystem and biogeochemical responses to climate change and variability. The recent identification of the 'non-steady-state' nature of the ocean carbon pump (e.g. in the North Atlantic: Schuster and Watson, 2007; Watson et al., 2009) and its response to climate raises concerns over its ability to continue to mitigate increasing atmospheric CO₂ levels (Le Quere et al., 2010).

Alongside the carbon cycle context, the structure and function of the ecosystem itself and how this responds to changing external conditions such as climate and fishing pressure is of particular importance as it relates to the economic and food security aspects of the exploitation of living marine resources (Stock et al., 2011), and also the societal drive to ensure a healthy marine environment. In Europe this is encapsulated in the Marine Strategy Framework Directive (MSFD) and the descriptors of Good Environmental Status therein.¹

Fig. 1a shows a schematic contrasting the shelf sea and open-ocean biological carbon pumps. In both cases the driver is the same, photosynthesis (P). However, the pathways of the fixed carbon to the point where it is isolated from atmospheric exchange on centennial time scales are very different. In the open ocean the respiration (R) that occurs as material sinks is a critical control, whereas in shelf seas the on/off-shelf transport is an important additional factor (Holt et al., 2009; Wakelin et al., 2012). In shelf seas much of the sinking carbon enters the benthos, but it is still largely respired and its long term fate largely depends on the relation between lateral transport (pathways and time scales) and the exposure to atmospheric exchange through vertical mixing. In both cases top-down control (grazing, G) has the potential to alter these pathways. This simple conceptual model belies the underlying complexity of the ecosystem (e.g. Fig. 1b), whereby individual organisms compete for resources at trophic levels from primary producers to top predators, leading to intricate ecological interactions. While this ecology has long been studied in the context of living marine resources (e.g. Hardy, 1924), its relationship to the carbon cycle is far from clear.

The North Atlantic is important and unique in several respects. It is a key component in the climate system due to the substantial poleward heat flux in its surface waters and the formation of inter-

mediate/deep water masses in its northern regions that help drive the Thermohaline Circulation (Macdonald and Wunsch, 1996). This region accounts for 23% of the global marine sequestration of anthropogenic CO₂ despite having only 15% of the area (Sabine et al., 2004). This arises because of the deep winter mixing forming intermediate and mode water masses combined with a lower Revelle factor than other mid- to high latitude regions. There is exceptionally high primary production (for a large ocean basin area) in the sub-polar gyre region (e.g. Carr et al., 2006) owing, among other factors, to significantly deeper winter mixed layers than other ocean basins (de Boyer Montégut et al., 2004). The ocean basin is bounded by shelf and marginal seas that support substantial economic activity (e.g. fisheries) and are themselves bounded by populous countries of Europe and Africa on the eastern side and the Americas on the west. Hence, impacts of large coastal cities and resource exploitation are acutely felt in this region, potentially mitigated by recent legislative action (e.g. MSFD). In contrast, the less developed countries of West Africa rely on artisanal fisheries as an important protein source (FAO, 2012) and so are highly vulnerable to changes in fish production in this upwelling region.

The particular question within the BASIN programme we aim to make progress towards answering are:

- What defines the biogeographic regions of the North Atlantic, and how might these change, and in what way and on what time scales might the ecosystem respond to these changes?
- What is the impact of top down control on the carbon cycle and phytoplankton community structure, how does this vary temporally and spatially, and under future climate and fisheries management scenarios?
- What are the pathways and ultimate fate of carbon sequestered by biological production, and how might these change?
- How does climate change and variability impact the ecosystem productivity, structure and function?

This requires a truly integrated modelling approach that spans from fisheries to plankton, and from the shelf seas to the open ocean. However, to achieve this we must, not only make significant advances in modelling individual systems, but also break down barriers in traditional scientific approaches, for example between modelling biogeochemical systems and modelling ecological systems, and between modelling the open-ocean and coastal-ocean. There is of course sound scientific reasons why different approaches are taken for each of these so full harmonisation is neither possible nor desirable, but to move towards the goal of an integrative system we must find the common ground and exploit the potential linkages.

Modelling approaches are context dependant; at each stage (physics, biogeochemistry, ecosystem, etc.) there are several complementary ways to explore the system differing in how the system is represented, in the time and space scales considered, and in the capability to address the particular questions at hand. Each will be a compromise in some sense, but also have particular advantages. Hence an integrative modelling approach needs to embrace this diversity and rather than providing a single mechanistic connection between drivers, impact and response, each component provides complementary evidence towards our understanding of the system's behaviour. Practical considerations inevitably limit the approach to a few discrete choices.

Within EURO-BASIN, we consider three configurations of a common physical model (Nucleus of a European Model for the Ocean, NEMO; Madec, 2008); three biogeochemistry/lower trophic level (LTL) models (ERSEM, MEDUSA and PISCES, described below); a regional scale Individual Based Model for the zooplankton species *Calanus* spp. coupled to a small pelagic fish (herring) population model (Utne et al., 2012; Utne and Huse, 2012); a spatially explicit

¹ <http://ec.europa.eu/environment/water/marine/ges.htm>

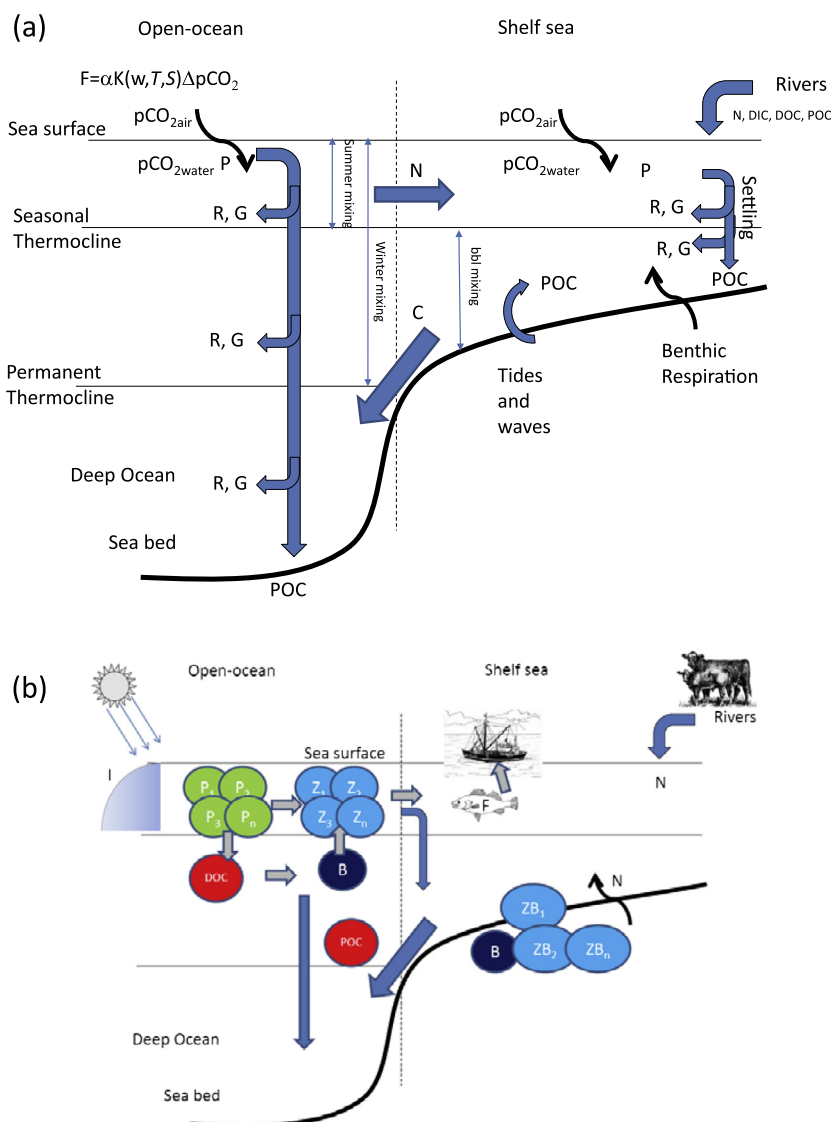


Fig. 1. Schematic of (a) open-ocean and shelf sea carbon pumps. Here shown for a downwelling shelf. In the upwelling case both C and N (nutrients) tend to be transported from the deep ocean to the shelf and (b) a simplistic representation of the marine ecosystem.

size-based model of open-ocean ecosystems, which aims to represent the joint effects of environmental variability and fishing on the structure and dynamics of pelagic ecosystems (APECOSM; Maury et al., 2007a, 2007b); and a spatially explicit population dynamics model (SEAPODYM; Lehodey et al., 2008; Senina et al., 2008; Sibert et al., 2012) predicting the effects of environment and fishing on key pelagic species, and including a functional representation of Mid-Trophic Level (MTL) groups (Lehodey et al., 2010) that are forage species of large oceanic predators (e.g., tuna, marine mammals, seabirds). We also consider a convective scale phytoplankton IBM. The particular combinations we consider here are listed in Table 1.

Specific issues we address in this paper are:

- Ocean physics in the open-ocean and shelf seas, and the coupling between the two (Section 'State of the art and challenges for physical models of biophysical interaction in the North Atlantic').
- Biogeochemistry and lower trophic level (plankton) ecosystems (Section 'State of the art and challenges for biogeochemical and lower trophic level models of the North Atlantic').

- Higher trophic levels including populations or functional groups of Mid-Trophic Level (micronekton) and top predators, and the coupling between these (Section 'Higher trophic levels modelling: state of the art, challenges and gaps').
- Experiment design for climate change impact simulations (Section 'Climate change projections for marine ecosystems of the North Atlantic').

Finally we conclude (Section 'Concluding remarks: integrating the EURO-BASIN models') by exploring how this approach can specifically address the questions identified above.

State of the art and challenges for physical models of biophysical interaction in the North Atlantic

The modelling of marine ecosystems is intimately linked to modelling marine hydrodynamics. The often quoted remark by Doney (1999) "biogeochemical models are only as good as the physical circulation framework in which they are set", implies that we must consider which aspects of the physics are important

Table 1
List of the EURO-BASIN suite of models and references.

Configuration	Physical model	LTL model	HTL model
Global 1/4°	NEMO ^a	MEDUSA ^b	
North Atlantic 1/4°	NEMO	ERSEM ^c PISCES ^d	SEAPODYM-MTL ^f IBM ^g APECOSM ^h
Northern North Atlantic 1/12°	NEMO-Shelf ^e	ERSEM ^c	
2D	Convection ⁱ	IBM	

^a Madec (2008).

^b Yool et al. (2011).

^c Baretta et al. (1995) and Blackford et al. (2004).

^d Aumont et al. (2003).

^e Maraldi et al. (2012) and O'Dea et al. (2012).

^f Lehodey et al. (2008).

^g Utne et al. (2012) and Utne and Huse (2012).

^h Maury et al. (2007a, 2007b).

ⁱ Kämpf and Backhaus (1998).

controls of the ecosystem, how well these are modelled and how this might be improved. When considering lower trophic levels (LTLs) and biogeochemistry, there are essentially three paradigms that mediated the biophysical interactions. First is the physiological response of the organism to the environmental conditions (e.g. temperature response of growth rates; [Eppley, 1972](#)). Second, mixing and transport processes control both the phytoplankton's exposure to light, hence triggering blooms ([Chiswell, 2011](#); [Huisman et al., 1999](#); [Sverdrup, 1953](#); [Taylor and Ferrari, 2011](#)), and the resupply of nutrients to euphotic waters. These generally act on seasonal or shorter time scales and are predominantly vertical processes, but it is appropriate to include mesoscale eddy and cross-frontal transport processes here. Finally, the basin scale transport sets the overall elemental budgets, e.g. of carbon and nutrients; a simple view of this is provided by the LOICZ² methodology ([Gordon et al., 1996](#)) of fluxes into and out of a well mixed box.

The modelling of higher trophic levels is considered in more detail in Section 'Higher trophic levels modelling: state of the art, challenges and gaps', however, it is worth briefly identifying some key aspects of the biophysical interactions applicable to that case. As soon as we are concerned with species, rather than 'functional groups' then issue of habitat arises, and whether or not it is suitable for a particular species across its life stages, depending on the behaviour of a population, time/space scale of change in the habitat and their ability to acclimate and eventually evolve to accommodate this change. This introduces other facets to the biophysical interaction that are not so important for biogeochemical/LTL considerations, namely: the 'bioclimate envelope' of the habitat ([Cheung et al., 2009](#)) and the connectivity and transport between regions of different habitats, i.e. what is the acceptable physical environment for a species and can an individual successfully move between regions of these characteristics as it changes life stage (and so environmental preference), given that these regions are themselves changing, on generally longer timescales? This then puts more detailed requirements on aspects of the physics to be modelled and understood, which are not necessarily required for modelling LTLs. Examples on the timing of stratification and spring blooms to determine prey availability ([Beaugrand et al., 2003b](#)), and on the details of currents to move larvae from spawning grounds (e.g. [Petitgas et al., 2013](#)).

While basin-scale oceanography and its climate variability drive the population dynamics of pelagic species ([Lehodey et al., 2006](#)), the mesoscale activity is also of interest to investigate in detail the behaviour of animals and to address key mechanisms

that need to be included in the new generation of population dynamics models. Various sources of biological data exist today (e.g., fishing data, acoustic, and satellite tags) that can be confronted to these multiple spatial and temporal scales ([Lehodey and Maury, 2010](#)).

Generally, the biophysical interactions put specific requirements on a hydrodynamic model used to simulate ecosystem processes, which in turn impose limits on the accuracy of the ecosystem model (e.g. [Sinha et al., 2010](#)). Ecosystem processes are often non-linearly dependent on material fluxes that are not constrained by external feedbacks, and so maybe more sensitive to internal model dynamics than aspects of the physics often used for model validation. The classic example is sea surface temperature (SST) and diapycnal mixing. While SST is an important parameter for coupled ocean–atmosphere modelling, successfully reproducing the field (compared with the plentiful observations) is not a particularly good guide to whether the mixed layer dynamics are well modelled, since the sensible heatflux will compensate for errors in this. In contrast, accurately modelling mixed layer properties is a necessary condition for a well modelled phytoplankton seasonal cycle; i.e. success (or otherwise) in modelling the ecosystem should be used as a guide to improving the physical model.

Horizontal resolution is crucial, and central to this is whether motions at the first baroclinic Rossby radius are permitted. This allows a class of phenomena that are either absent or poorly represented in coarser resolution models to be simulated, specifically: coastal upwelling, mesoscale eddies and internal tides; all of which have important consequences for the modelled ecosystem. The scale for many important processes is the first internal Rossby radius of deformation (R_1 ; [Fig. 2](#)). The eddy scale (L_o) is known to vary linearly with R_1 from both empirical altimeter based studies, $L_o \sim 1.7R_1 + 86$ km, ([Stammer and Boning, 1996](#)), and theoretical and laboratory studies ($L_o \sim \pi R_1$) such as those of [Griffiths and Linden \(1982\)](#). Similarly the lateral scale of upwelling velocity is also, R_1 ([Huthnance, 1995](#)); this can be shown analytically for the case of a vertical wall, but R_1 decreases rapidly at the shelf edge so resolving the deep ocean value should be seen as a lower bound. Internal tides have a wavelength $\sim R_1 f / \omega$, so show a similar pattern to the Rossby radius, but without the strong increase towards the equator. Internal tides and upwelling require several grid cells per Rossby radius, whereas mesoscale eddies can be permitted at lower resolution owing to the multiplier in their scaling. However, upwelling will still occur in models that do not resolve this scale, but it will not be well represented; internal tides and eddies will simply be absent. The ORCA series of global NEMO model configurations includes 1/12°, 1/4° and 1° versions, with typical grid size in the North Atlantic of, respectively, 6 km, 18 km, and 72 km. From [Fig. 2](#), the 1/12° configuration can be characterised as being eddy resolving in the subtropical gyre ($e = R_1 / \Delta x > 4$), comfortably eddy permitting in subpolar gyre and nordic seas ($e \sim 1-4$), but eddy excluding on-shelf ($e < 1$). The 1/4° model reduces this ratio by a factor of 3 so is eddy permitting in sub-tropical gyre, marginally eddy permitting in sub-polar gyre, otherwise eddy excluding. Alongside the dynamical scales, the resolution of geographic scales (bathymetry and coastline) is important in determining the local of the currents (such as the Gulf stream) and between basin transport.

To illustrate the importance of horizontal resolution, results are presented for three models with comparable physics but different horizontal resolution in the ORCA series of NEMO models, along with climatological observations, for surface current speed ([Fig. 3](#)), mixed layer depth (MLD; [Fig. 4](#)), and sea surface temperature (SST; [Fig. 5](#)). Ecosystem models are, to some extent, tuned to a particular representation of the physical environment, i.e. the time/space scales and process representation. Ideally this would be the best physical representation available, but inevitably

² Land Ocean Interaction in the Coastal Zone; <http://www.loicz.org/>

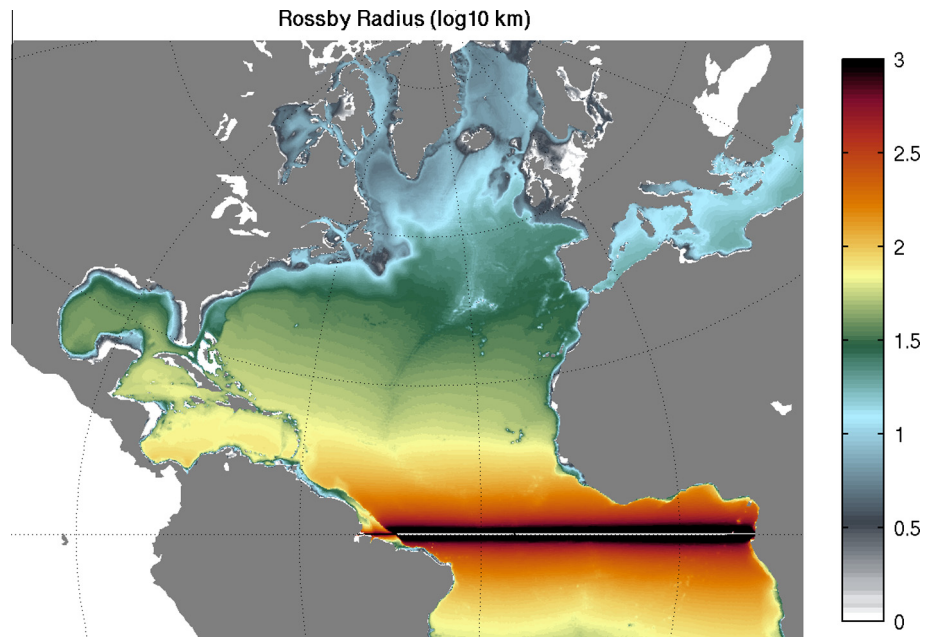


Fig. 2. The first baroclinic Rossby Radius (log10 km) from the ORCA083 model. This is calculated using a shooting method from an average annual cycles of monthly mean density values. The maximum value is shown here.

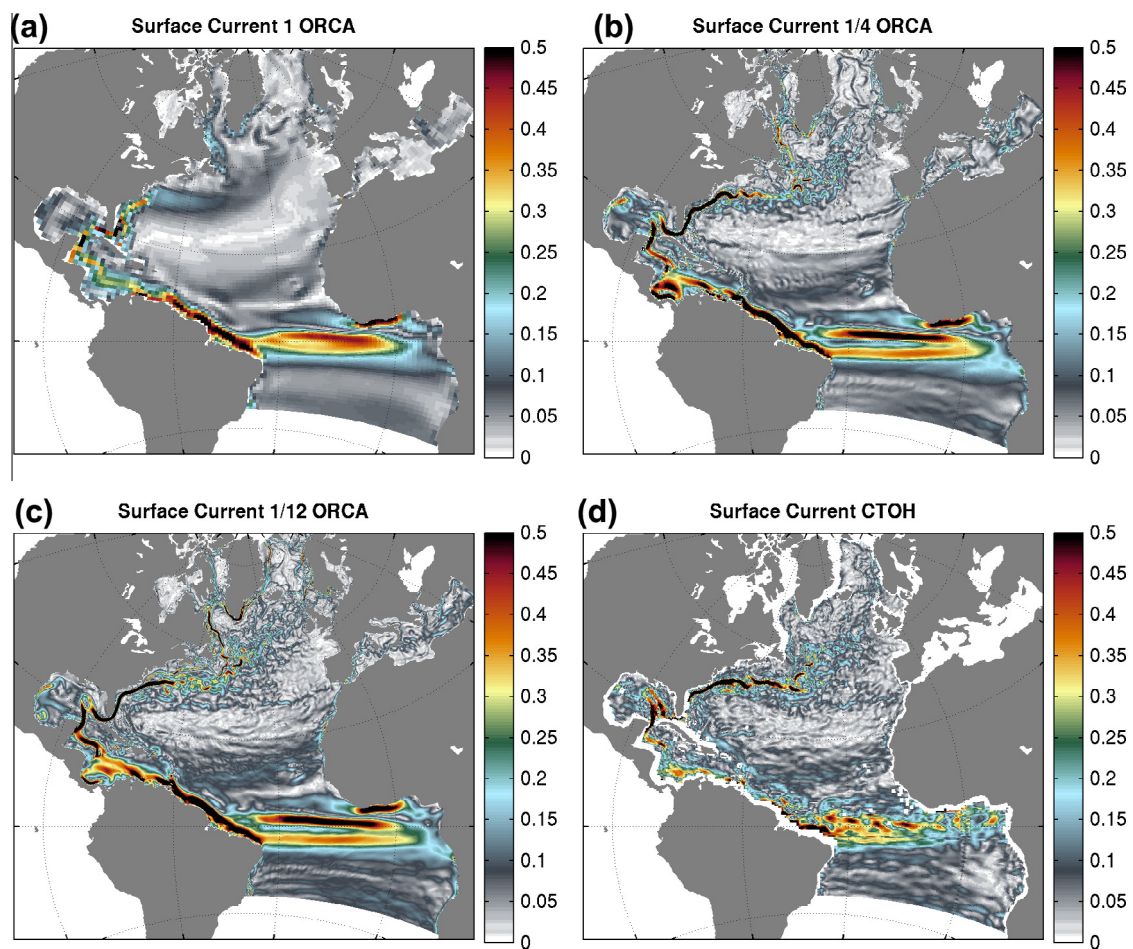


Fig. 3. Mean surface current for 2006 in 3 global NEMO simulations: (a) 1°, (b) 1/4°, (c) 1/12°, (d) observations (CTOH; [Sudre and Morrow, 2008](#)).

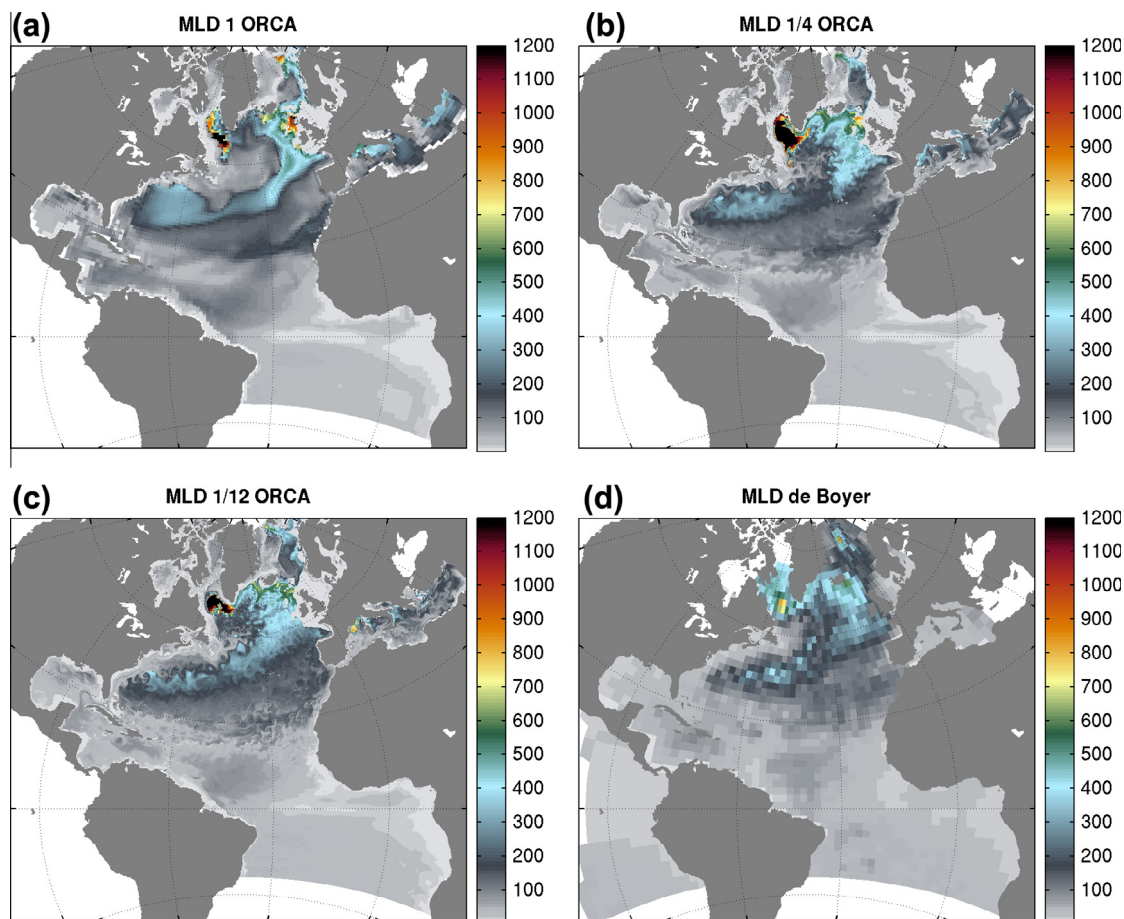


Fig. 4. Mean March 2006 MLD based on a 0.2 °C density criterion in 3 global NEMO simulations: (a) 1°, (b) 1/4°, (c) 1/12°, (d) Climatological observations (de Boyer Montégut et al., 2004).

practical considerations limit this, and ecosystem models tend to be developed and tuned on the coarser end of this scale. This potentially leads to error compensation and over-tuning of the ecosystem model to compensate for inadequate physics (Popova et al., 2006). Hence a detailed analysis is required of how different aspects of the physics are modelled and how these constrain the ecosystem.

Transport processes in the North Atlantic

Of the many currents forming the gyre circulations in the North Atlantic, the Gulf Stream and its extension into the North Atlantic Current and Azores Current is the most prominent. The currents on the eastern side (e.g. the eastern margin slope current; Pingree et al., 1999; Souza et al., 2001) are weaker, but none the less form important components of the circulation. The Gulf Stream path has particular importance to the surface fluxes, for example Eden and Oschlies (2006) in studying OCMIP-2 model biases found that “[the biases] lead to a large range of simulated total air–sea carbon flux patterns and in consequence a large uncertainty in simulated oceanic uptake of anthropogenic CO₂”.

A central issue in modelling the circulation of the North Atlantic is to achieve an accurately located Gulf Stream separation at Cape Hatteras, and subsequent current pathways, particularly the Northern Exursion. This has been the subject of substantial effort and current thinking is that many factors, including coastline, bathymetry, barotropic–baroclinic coupling with the deep western boundary current, and mesoscale eddies, control this circulation

(see Hecht and Smith, 2008 and references therein). Similarly, many modelling factors play a role in producing a realistic Gulf Stream separation. There is great sensitivity to subgrid scale parameterisations, boundary conditions (or global versus regional domains) and choice of dissipation operators (Chassignet and Marshall, 2008). Bryan et al. (2007) suggest the Gulf Stream is greatly improved as the horizontal resolution is reduced below 10 km, thus resolving the first baroclinic Rossby radius and also more accurately representing the bathymetry and coastline. This is clearly seen in Fig. 3 in terms of the location of the surface maximum and Fig. 5 in terms of the location of the temperature front. As far as numerical solution methods are concerned, Barnier et al. (2006) found in a 1/4° study, that by implementing partial cells for the geopotential vertical coordinates, and an energy and enstrophy conserving scheme for solving the momentum equation, they were able to improve the flow patterns in the North Atlantic. But given all these factors, the key determinant in accurately representing the circulation is model resolution. For example, Fig. 3 shows the non-eddy permitting model (1° ORCA), not only underestimates the strength of the Gulf Stream currents by ~4-fold, it separates from the coast too far north and is too zonal in direction. The 1/4° ORCA substantially improves the speed, but it is only at 1/12° that its path is accurately modelled.

While progress has been made through subgrid scale mixing (e.g. Gent and McWilliams, 1990; see below) and topographic representation (e.g. immersed and porous boundary approaches; Adcroft, 2013; Tseng and Ferziger, 2003), they are far from the accuracy achieved by refined resolution, and also miss many of

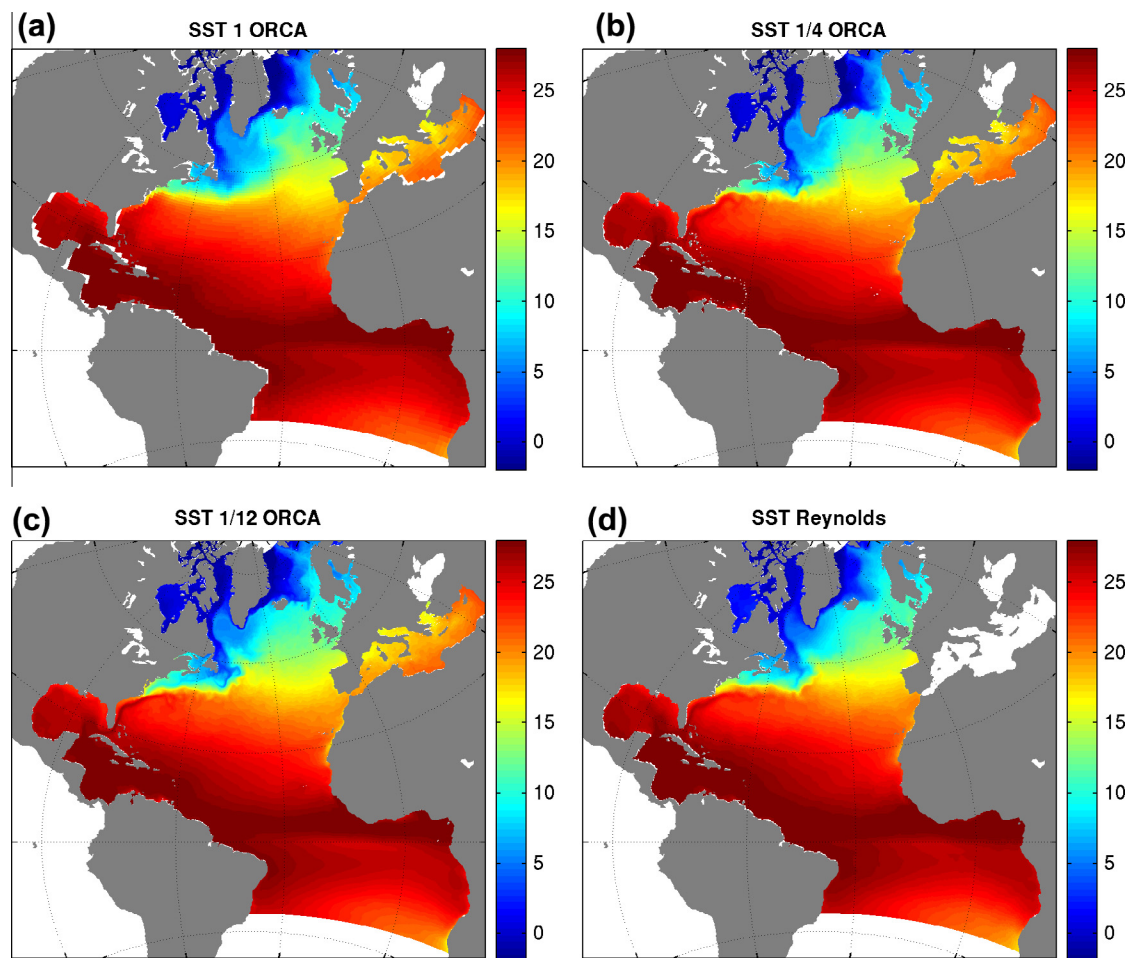


Fig. 5. Mean SST for 2006 in 3 global NEMO simulations: (a) 1°, (b) 1/4°, (c) 1/12°, (d) Observations (Reynolds SST; Reynolds et al., 2007).

the nuanced processes such as non-local effects of eddies. Some caution is needed as increased eddy activity in a model can also result in spurious enhanced diapycnal mixing (Griffies et al., 2000).

The position of the large scale currents also impacts on the relevant water mass formation, overturning circulation and hence the solubility carbon pump. The model intercomparison study by Treguier et al. (2005) suggests the meridional overturning is primarily influenced by deep overflows, while the horizontal circulation of the gyre is influenced by both deep overflows and deep convection. They suggest that difference in deep convection patterns in the Labrador Sea are related to differences in their barotropic transport at Cape Farewell.

Aside from the Gulf Stream and sub-polar gyre, an important feature of the circulation on the western side of the North Atlantic is the coastal current from the northern Labrador shelf to Cape Hatteras (Loder and Petrie, 1998), formed by freshwater from a combination of ice melt and riverine sources. While there is considerable freshwater loss to the open-ocean along this path there is also evidence of some continuity of flow. In contrast many of the shelf seas on the eastern side of the basin lack such a strong advective component, the Norwegian coastal current being a notable exception. Generally, coastal currents carry terrestrial influence (e.g. freshwater, nutrients, CDOM, Alkalinity) far from their source and are an important inter-basin transport mechanism e.g. linking the Baltic, via the North Sea and Norwegian Sea with the Barents Sea in the Arctic. Their accurate representation, particularly the lateral transport by eddies (Johannessen et al., 1989), requires the resolution of

the on-shelf Rossby radius and so challenges many model systems. The North Atlantic Drift joins the eastern boundary slope current in the Faero-Shetland channel, another region of strong eddy activity (Sherwin et al., 2006).

Mesoscale and submesoscale eddies

The stratified ocean is naturally full of eddies arising from baroclinic instability and the inverse energy cascade (Polvani et al., 1994). The North Atlantic is a region of intense eddy activity and the growth of satellite based Earth Observation, particularly altimetry but also SST and ocean colour, over the last decades has lead to a substantial improvement in understanding of the eddy field in the North Atlantic (e.g. Ducet et al., 2000). Bryan and Smith (1998) clearly demonstrate the importance of resolution in accurately reproducing this eddy field using models of 0.4°, 0.2°, 0.1° resolution. However, the role of subgridscale parameterisations and numerical methods is more subtle. There is a growing appreciation of the importance of the eddy field in determining the physical oceanographic properties of the basin, both the mean and fluctuating components, at the surface and at depth. A correct eddy field is crucial in setting key features such as the Gulf Stream separation, northward penetration, formation of the Azores current, the subpolar front and the general gyre circulation (Hecht and Smith, 2008). Eddies play a particularly important role in mixing, for example determining mixing and stratification in the Labrador sea through baroclinic, baroclinic–barotropic and convective (sub-

mesoscale) eddies (Chanut et al., 2008), and in setting the flow of energy between the density field and the mean circulation.

Models of resolution that permits or resolve motions at the Rossby Radius (see above) have the potential for a realistic eddy field and represent a ‘threshold to be crossed’ (Hecht and Smith, 2008) in ocean modelling capability, which has now been crossed in many dynamical studies. However, as is discussed further below, ocean models used for biogeochemical studies, and especially those used as the ocean components of an Earth Systems Model, have not generally crossed this threshold, despite the well-established link between mesoscale eddies and oceanic production. The computational constraints are simply too great, since the CPU costs increase as $(1/\Delta X)^3$ and storage costs as $(1/\Delta X)^2$. Hence, the subgrid scale parameterisation of mesoscale eddies represents an important area of research, and the North Atlantic has provided the natural laboratory for this. Of particular note are the parameterisation of Gent and McWilliams (GM; Gent et al., 1995) and Fox-Kemper et al. (2008), which attempt to account for the mean transport component of eddy flux (the “bolus velocity”) and the up-gradient eddy transport (Eden, 2007). The use of GM has greatly improved the physical simulations of non-eddy resolving models, but many problems remain notably in the Gulf Stream Separation and the Northwards Gulf Stream excursion. The impact of this on the modelled biogeography and biogeochemical process in the North Atlantic has yet to be established and this is an important consideration in EURO-BASIN.

In the case of eddy permitting models, subgrid scale parameterisation focuses on the submesoscale and is largely an element of model stabilisation and tuning, with the aim being to achieve both accurate statistics in the eddy field and well represented mean properties. Models tend to employ combinations of Laplacian and biharmonic operators (Chassignet and Garraffo, 2001; Hecht et al., 2008); however, a well justified parameterisation based on submesoscale physics (e.g. Lévy et al., 2010) is currently lacking.

Subgridscale parameterisation is a particular issue in coupled ocean–shelf models since the dominant scales ($\sim h^{0.5}$) change dramatically at the shelf edge to the extent that a model may change from being eddy permitting in the open-ocean to non-eddy permitting on-shelf. This has two specific implications: the interpretation of results in the two regimes needs to take this into account and the physical interpretation of ‘sub-grid scale’ changes, and so should the parameterisation (e.g. Wakelin et al. (2009) use a simple depth dependent horizontal eddy diffusivity/viscosity). However, as noted by Holt and James (2006), the treatment of horizontal diffusion is “one of the least well-established areas of shelf-sea modelling and has received scant attention compared with the extensive literature on vertical turbulent transport (see e.g. Baumert et al., 2005)”.

Mixing processes in the North Atlantic

More than in any other ocean region the North Atlantic is characterised by its diverse range of mixing regimes, which largely set the scene for its biophysical interaction, and so need to be carefully considered in any model. The energetic mixing/vertical transport processes include tides, wind mixing, mesoscale eddies, deep winter convection, and coastal upwelling.

The North Atlantic is a region of exceptionally energetic tides and these are amplified on the continental shelves of the North, Celtic, and Irish Seas (on the eastern side of basin) and Bay of Fundy and Hudson Straits (on the west) to give the largest tidal amplitudes globally. Shelf seas, e.g. North Sea and Georges Bank, show patterns of well mixed and seasonally stratified waters set by the criterion of Simpson and Hunter (1974). This in turn sets the benthic/pelagic recycling characteristics of these seas and the balance between light and nutrient limitation. Modelling tides at a basin and shelf

scale is comparatively straightforward given their approximation to coastal trapped waves under linear conditions (see Holt et al., 2014 and references therein), and basin scale tides are well established from inverse models derived from satellite altimetry (Egbert et al., 1994). Tides, and other high frequency barotropic waves, are generally not included in global and basin scale models, but their inclusion directly or at least through a parameterisation (e.g. Simmons et al., 2004) is a prerequisite for a model that aims to simulate both the open ocean and shelf sea regimes. In a model with a fixed vertical grid including tides would be expected to result in spurious diapycnal mixing, and hence deterioration of water mass properties. Time varying vertical coordinates and a re-mapping vertical advection approach may address this (James, 2000), and this approach has recently been incorporated into the NEMO model.

A primary consideration in tidal modelling is that the benthic boundary layer is well resolved. In mid- and high latitude regions the cyclonic component of the boundary layer is very thin (Soulsby, 1983). Along with the need to resolve sharp pycnoclines, this is one motivation for the use of terrain following coordinate models in tidally active shelf seas, such as those bordering the North Atlantic. Difficulties tend to arise where the boundary layer meets stratification and accurately modelling the resulting sporadic diapycnal mixing (e.g. spring-neap tidal pumping; Sharples et al., 2001), is problematic.

The Northern North Atlantic is an exceptionally windy region, comparable to the northern North Pacific and Southern Ocean in annual mean wind stress (e.g. Josey et al., 2002). This leads to exceptionally deep mixed layers, which can be particularly challenging to model (Fig. 4). While monthly mean winds stresses can provide a reasonable representation of the seasonal evolution of the mixed layer depth, it is well known that accurately representation of the mixed layer dynamics requires high frequency atmospheric forcing, ideally resolving the inertial period ($1/f$), otherwise wind stresses can be significantly underestimated and phenomena such as inertial shear spiking (Rippeth et al., 2009) are not represented.

Vertical mixing models fall into three categories: mixed-layer parameterisations (e.g. KPP; Large et al., 1994), one-equation turbulence models with a single equation for turbulent kinetic energy (TKE) and prescribed mixing length (Holt and James, 2001; Madec, 2008); and second-moment models with a second dynamic equation for some combination of TKE and mixing length (e.g. for the turbulence dissipation in k-epsilon models; Umlauf and Burchard, 2005). A particular feature of the North Atlantic is the deep convection in northern regions. In the first two of these categories this is treated by an iterative ‘convective adjustment’ process. While this is reasonably successful at modelling the mixed layer depths (Fig. 4), the actual turbulence levels occurring with the convection are not necessarily appropriate, particularly at the surface where mixing lengths are limited by the ‘Law of the wall’ ($l \sim kz$). A second-moment model (e.g. Generic Length Scale; Umlauf and Burchard, 2003) does not have this limitation, and so is likely to better represent critical turbulence levels (Huisman et al., 1999); although it still only includes local down-gradient (diffusive) turbulent transport.

All three classes of turbulence models have varying success in modelling mixed layer depth, and given its biological importance significant effort goes into tuning the model to better represent this property. This is a case where the more empirical models have an advantage; the models based on turbulence theory have stronger constraints on acceptable parameter values, for example the closure model of Canuto et al. (2001) has ‘no adjustable parameters’. While this is theoretically pleasing, it is problematic in practice and tends to lead to add-on such as mixing length limiters (Galperin et al., 1988; Holt and Umlauf, 2008), arising because of the essentially non-isotropic nature of stratified turbulence

(isotropy is an underlying assumption in the formulation). The local nature of the underlying formulation is also an issue; transport of turbulent properties is only treated as a simple vertical diffusion. While the non-local issue could be addressed with representation of transport processes such as Langmuir cells and convection, care is needed owing to a more pressing issue, namely numerical diffusion. Advection schemes that are non-dispersive (i.e. positive definite) are generally diffusive. This gives rise to spurious numerical vertical mixing than can exceed the realistic levels of physical mixing (Burchard and Rennau, 2008); the last thing many ocean models need is more vertical mixing. Hence, alongside the extensive observational effort in the North Atlantic to improve the parameterisations of mixed layer properties, e.g. in the UK OSMOSIS project, considerable modelling effort is required to minimise numerical diffusion so as to accommodate this improved knowledge, for example building on the methods of Colella and Woodward (PPM; 1984) and Prather (1986).

While, the underlying processes determining the mixed layer depths are essentially vertical, they are modified by horizontal transport to the extent that the mixed layer depths are strongly sensitive to horizontal resolution (Fig. 4). There is a clear improvement between the $1/4^\circ$ ORCA and 1° ORCA (e.g. in NE Atlantic), accepting anomalously mixed layer in the Labrador Sea in the latter. The picture is further improved in the $1/12^\circ$ ORCA model.

Ocean-shelf coupling

The challenge of modelling ocean-shelf coupling lies in the superposition of first-order changes in water depth and a range of locally specific dynamical processes (Huthnance, 1995). From an ecosystem point of view coastal upwelling is the most prominent process in terms of ocean-shelf coupling. While the most productive eastern margin upwelling systems globally are not in this region, the West African and Iberian upwelling systems make an important contribution to the basin wide production (Carr et al., 2006). Again this is primarily an issue of scale. The primary upwelling circulation requires the (deep ocean) first Rossby Radius to be resolved, whereas the complex secondary circulation, filaments (Peliz et al., 2002) and eddy effects (Gruber et al., 2011) require significantly finer resolution.

Internal tides provide an important mechanism for enhanced mixing at the shelf-edge, which have been particularly difficult to include in coupled ocean-shelf model. The difficulty arises because of spurious diapycnal mixing at the steep topography. Other specific numerical issues for terrain following coordinate models are horizontal pressure gradient (Shchepetkin and McWilliams, 2003) and horizontal diffusion (Beckers et al., 2000) calculations at the juxtaposition of sloping coordinates, topography and stratification.

The relative strength of ocean-shelf exchange, riverine and atmospheric inputs, sets the elemental inventory on-shelf. These are augmented by biogeochemical processes such as denitrification and nitrogen fixation (Hydes et al., 2004). The adjustment time of shelf seas to oceanic conditions depends on this ocean-shelf exchange and ranges from days in narrow up-welling shelves to many years on shelves with limited exchange and weak circulation (e.g. ~ 6 years in the Celtic Sea; Hydes et al., 2004). Holt et al. (2012a), in a Northeast Atlantic model simulation find reasonable agreement to the steady state 'LOICZ' approach for nitrate. However, the assumption of a well mixed basin behind this are called into question when salinity is considered: the observed ocean-shelf salinity difference underestimates the ocean-shelf exchange by a factor of 4 compared with the values given by Huthnance et al. (2009); indicating much of the transport occurs without significant lateral mixing with fresher coastal water.

Modelling North Atlantic physics: coast to ocean

Open-ocean and coastal-ocean hydrodynamic models have had a somewhat different evolutionary history, resulting from the different scales and classes of problems in the two regimes. Coastal-ocean models have focused on the requirement of the vertical coordinate systems to resolve the benthic boundary layer, a free surface calculation that can accommodate large amplitude waves, turbulence models capable of simulating multiple boundary layers and the need for accurate open boundary conditions. Notable examples in the North Atlantic context are: the ~ 1.8 km POLCOMS European shelf model of Holt and Proctor (2008) and the multiscale FVCOM model developed for US GLOBEC (Chen et al., 2007). In contrast, open-ocean models have focused on the need to preserve water masses during long integrations, the representation of meso-scale eddies (resolved or parameterised), and horizontal coordinate systems on the sphere. These include both regional models such those used in the DYNAMO project (Willebrand et al., 2001) and the NATL12 North Atlantic Model (Treguier et al., 2012), and global models where the focus of analysis has been the North Atlantic (see Hecht and Smith, 2008).

The choice of horizontal and vertical resolution remains a key determinant of model quality and also of computational and data handling costs. At the basin wide scale a clear improvement in eddy kinetic energy and Gulf Stream path has been demonstrated as grids are refined. However, the models we consider here are far from convergence, i.e. reaching the aspirational condition of computational fluid dynamics that the solution is no longer dependent on grid resolution or subgrid scale parameterisation. Those studies that have hinted at convergence (Hecht and Smith, 2008) have a substantially fine resolution than considered here.

In the shelf sea context a systematic comparison of 9 models covering (at least) the North Sea with common forcing do not show a clear improvement with resolution (from ~ 3 km to 20 km) when compared with temperature and salinity observation from the ICES data base (Delhez et al., 2004). The introduction of stochastic properties into the model and the nature of the data (point profiles) means increasing resolution does not necessarily improve such model-data comparisons. Whether it leads to a 'better' model therefore depends on the questions being asked of the model, and requires a more detailed investigation.

Global and basin scale models are now routinely run at resolutions similar to historical shelf sea models (~ 10 's km; e.g. Backhaus and Hainbucher, 1987), and so are capable of representing (albeit crudely) on-shelf processes given appropriate process formulation. Similarly, larger area shelf sea models are now run nested within global models to investigate ocean-shelf coupling (Holt et al., 2012a) and basin scale response (Chaudhuri et al., 2011); and indeed their inadequacies in deep ocean regions are becoming more apparent (Holt et al., 2012b). Hence, it is now appropriate to look to a unified ocean-shelf modelling system and to blur the distinction between the two. The scientific benefits of this are to remove the uncertainties associated with open-boundaries and to allow two-way exchange of information and material. The NEMO model system (Madec, 2008) provides the opportunity for such an approach, owing to its recent developments for shelf sea applications (Maraldi et al., 2012; O'Dea et al., 2012). The practical benefits are through working with a common code structure, traceability between open-ocean and shelf sea model characteristics, and through the exchange of ideas between the two scientific communities. These benefits are inevitably offset by the challenges of unified modelling of two distinct marine environments that largely lead to the distinct evolution of ocean and shelf sea modelling in the first place. Simply having the modelling capability in place in a single system is not sufficient to address the ocean-shelf coupling issue. Moreover, computational issues

(CPU and data volume) still lend significant benefits to small area regional models, where these are sufficient for the problem at hand.

Physical modelling in EURO-BASIN

We work with three configurations at two scales: $1/4^\circ$ Global and North Atlantic and $1/12^\circ$ Northern North Atlantic. The results above (Figs. 3–5) show significant improvement as resolution is increased and the focus of much of the modelling in EURO-BASIN will be a common $1/4^\circ$ North Atlantic configuration based on NATL025 (Levier et al., 2007); i.e. with significantly improved physics over the 1° model. However, while this configuration approaches the ‘resolution threshold’ identified above it does not cross it. Hence, novel physical model development in EURO-BASIN focuses largely on the development of a $1/12^\circ$ Northern North Atlantic Model (NNAM) building on the ORCA083 NEMO configuration. This model will be used coupled to the European Regional Seas Ecosystem Model (ERSEM) and able to explore the effects of crossing this threshold on biogeochemical processes and biogeography of the North Atlantic at Basin scales and with realistic forcing.

Our starting point for NNAM is an extraction from global model spanning the North Atlantic 25°N to 70°N chosen to encompass the sub-polar gyre and a large part of the sub tropical gyre. Particularly, the Gulf Stream initiation provides a well posed south-western boundary condition. This model is initially configured in an identical fashion to ORCA083 apart from the use of lateral boundary conditions. Data for these are taken from the ORCA083 model. We then incrementally incorporate features appropriate to the improved representation of coastal seas, which are now described.

The representation of the vertical dimension is a contentious issue across all of ocean modelling (Willebrand et al., 2001) and one we specifically consider in EURO-BASIN, particularly in relation to ocean–shelf coupling. Geopotential coordinates are the mainstay of open-ocean models, but the refinement of these through partial steps (Barnier et al., 2006) and shaved cells (Adcroft et al., 1997) to better represent the bathymetry and barotropic modes is an important development. In EURO-BASIN we exploit the generalised vertical coordinate system in NEMO to explore the use of hybrid terrain following–geopotential coordinates to gain the advantages of both in a basin scale model spanning the deep ocean to the coast.

Tidal dynamics both from gravitational forcing and open boundary conditions will be implemented, following the NW European shelf application of NEMO (O’Dea et al., 2012), along with the Generic Length Scale turbulence model (GLS; Umlauf and Burchard, 2003) with the parameters suggested by Holt and Umlauf (2008). The ERSEM ecosystem model will be forced by river and atmospheric nutrient inputs and inherent optical property specification following Wakelin et al. (2012). This will realise a fine resolution hybrid ocean–shelf model of the northern North Atlantic clearly traceable to state of the art ocean and shelf sea models. This will allow us to explore the impact of the many resolution dependent issues on the ecosystem.

Fig. 6 shows an early stage in this process – a section across the eastern North Atlantic at 51°N , for the global and regional $1/12^\circ$ models differing only in that the latter uses the GLS turbulence model and is forced by boundary conditions from the former. This demonstrates an improved thermocline depth and thickness using the GLS model and corresponding parameters. A further detailed investigation is required on the implications of this scheme particularly in the context of deep winter mixing and seasonality in tidally mixed waters, and whether it degrades other aspects of the solution.

State of the art and challenges for biogeochemical and lower trophic level models of the North Atlantic

The overarching concept of BASIN requires the investigation of the biogeochemistry of both shelf seas and the open ocean along with the connections between them at the scale of the whole North Atlantic. Alongside temperature and currents, primary production at the base of the food web, zooplankton as a food sources for fish and dissolved oxygen concentration (O_2) are important properties that need to be realistically simulated to drive higher trophic level models. A key question is how will climate variability and change, and its consequences, influence the seasonal cycle of primary productivity, O_2 , trophic interactions, and fluxes of carbon to the benthos and the deep ocean? Representing biogeochemistry and ecosystems in ocean general circulation models (GCMs) and shelf sea models remains an ongoing challenge given the complexity and diversity seen in marine systems. Nowhere is this more the case than in the North Atlantic, with its seasonal mid- to high latitude regimes characterised by ‘boom and bust’ spring bloom dynamics, and oligotrophic subtropical gyres dominated by microbes. The basin is surrounded by diverse marginal regions and shelf seas. These include eastern boundary upwelling regions, regions strongly influenced by western boundary current intensification (and hence mesoscale eddy activity impinging on-shelf), broad tidally active shelves (with strong benthic–pelagic coupling), polar seas where seasonal ice cover dominates the biogeochemical cycles, and regions dominated by riverine inputs and coastal current, where terrestrial inputs of nutrient and CDOM play an important role.

Historically in a similar fashion to the physical modelling community, the open ocean biogeochemical and shelf seas ecosystem modelling communities have developed independently focused around different goals, but are now starting to converge. Driven initially by the international JGOFS program (Hansen et al., 1999) and more recently the climate change agenda, the open ocean modelling has primarily focused on biophysical interactions and the quantification of the biological carbon pump (e.g. Aumont et al., 2003; Fasham et al., 1990; Sarmiento et al., 1993; Yool et al., 2011). At the same time, the shelf seas modellers were developing models with an initial focus on nutrient cycling and eutrophication in the coastal zone (e.g. Allen et al., 2001; Franks and Chen, 1996; Schrum et al., 2006; Skogen et al., 1995; Tett et al., 1994). Alongside this, the European Regional Seas Ecosystem Model (ERSEM) was being developed as, what in today’s jargon is termed, an ‘end to end’ model for the North Sea (Baretta et al., 1995), originally representing a foodweb that included plankton, benthic fauna and fish.

Underlying all these models is a commonality of approach in that all the biological components have been aggregated and abstracted into functional groups, which represent the ecosystem in terms of pools of elemental mass, rather than individual organisms or species. Marine ecosystems are complex non-linearly connected systems with emergent behaviour that is not simply a function of their physical environment. Hence, an ecosystem model should ideally have sufficient ecological flexibility to allow this behaviour to manifest (e.g. to permit the key competitions for resources in the system). In all the models considered here the trophic connections (i.e. the foodweb) are fixed and the interactions are defined with fixed but uncertain parameters, which are strongly dependent on the definition of the functional groups. The models produce trophic interactions that adapt to their physical environment by channelling mass through different components of the model ecosystem, but are limited by the inability of a fixed foodweb to self-organise.

The first attempt to meet the challenge of modelling basin-scale ecosystem dynamics in the North Atlantic using an explicit ecosys-

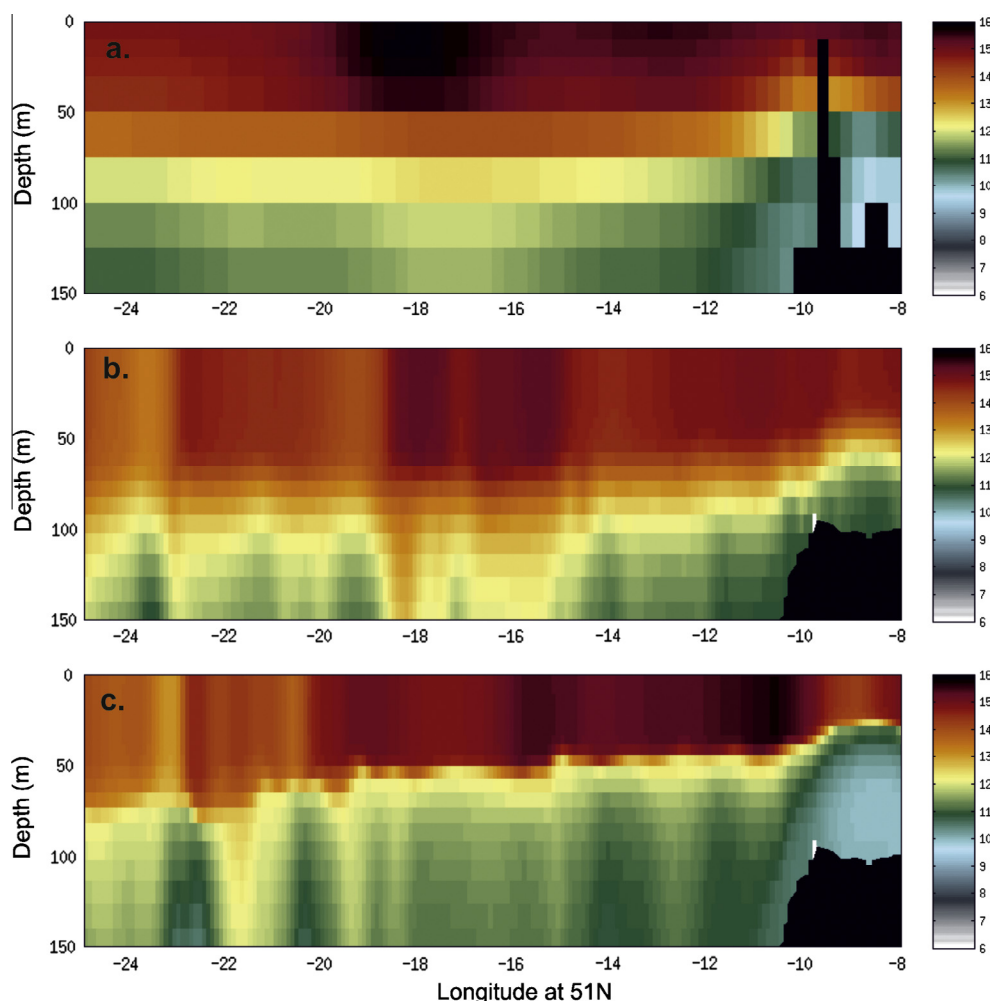


Fig. 6. Upper ocean temperature section at 51°N August: (a) Observation (WOA), (b) 1/12° Global, (c) 1/12° EURO-BASIN Northern North Atlantic Model.

tem model in combination with a GCM was carried out 20 years ago by Sarmiento et al. (1993). Using a NPZD model Fasham et al. (1990) coupled to a 2° resolution GCM, comparison of predicted phytoplankton with satellite-derived chlorophyll showed “excellent agreement ... in terms of basin scale pattern”, (Sarmiento et al., 1993). Results highlighted how physical forcing drives spatial patterns in marine ecosystems, as had been previously demonstrated in regional modelling studies (Hofmann, 1988; Walsh et al., 1988; Wroblewski, 1977). This early work supports the paradigm of biophysical interaction through physical controls of nutrient resupply, in this case by seasonally varying mixing and upwelling. Nevertheless, there were problems, including the timing and magnitude of the spring bloom in northern latitudes, phytoplankton concentrations an order of magnitude too low in the subtropical gyre and too high in the equatorial upwelling region. The authors attributed most of these model-data mismatches to problems associated with the physics of the GCM, and hence the focus in Section ‘State of the art and challenges for physical models of biophysical interaction in the North Atlantic’. The importance of the ecosystem representation was, however, also acknowledged. In an accompanying paper in which a detailed analysis of the GCM results for Bermuda station “S” was carried out, Fasham et al. (1993) noted the critical importance of the zooplankton in understanding ecosystem dynamics and of the need for observational data to underpin the associated parameterisations. All of these issues still persist with today’s models, in spite

of higher resolution physics, more complex foodweb descriptions and improved parameterisations based on better understanding of the underlying processes. We explore below how biogeochemical modelling of the North Atlantic has progressed since this pioneering work, and what the new challenges are, given the need for an integrated approach that permits prediction of both lower trophic levels and associated biogeochemistry, and transfer to high trophic levels such as fish.

The physical controls

Despite increases in the computing power during the last 20 years, most basin- or global-scale GCMs that incorporate biogeochemistry are still run at a resolution of $\sim 1^\circ$; this is particularly apparent in the array of Earth Systems Models used in the CMIP5 process (Taylor et al., 2012). Most regional shelf seas applications are run at scales of order $1/10^\circ$, i.e. an equivalent physical representation to 1° between 4000 m and 40 m given that the Rossby radii crudely scale with $\sim H^{0.5}$. Hence, many of the problems whereby biogeochemical predictions are compromised by model physics remain, notably excess chlorophyll in equatorial upwelling areas, too low production in the oligotrophic gyres (e.g. Yool et al., 2011) and in the shelf seas timing (to early) and depth of stratification (to shallow; Holt et al., 2005). While, the paradigm that stratification controls nutrient supply and hence phytoplankton production generally holds on seasonal timescales, it breaks down

on inter annual timescales in that there is ‘at most a weak correlative relationship’ between inter annual variability in upper ocean stratification and primary production in the subtropical gyre of the North Atlantic (Lozier et al., 2011). It is not sufficient to just consider the barrier preventing nutrient resupply, the processes driving this must also be considered, namely the wind and buoyancy driven mixing and lateral transport.

Given the importance placed on mesoscale features in the physics of the North Atlantic (as discussed above), one obvious solution is to increase the grid resolution. The importance of mesoscale physics (e.g. eddies and upwelling filaments) in controlling new production and associated biogeochemistry is well-known (e.g. Gruber et al., 2011; Levy et al., 2012; McGillicuddy et al., 1998). Oschlies and Garçon (2000) used a $1/3^\circ$ North Atlantic GCM in combination with an NPZD model and found that, despite representing eddy-induced enhancement, primary production remained too low in the subtropical gyre. It is possible to go yet further, as it is known that submesoscale vertical motions can have profound effects on the structure and function of plankton ecosystems (Allen et al., 2005, 2004; Perruche et al., 2011). Increasing resolution to represent submesoscale physics, Lévy et al. (2010) used a $1/54^\circ$ circulation model to study gyre circulation in a closed rectangular section of the North Atlantic. A strongly turbulent eddy field emerged that significantly affected the overall circulation pattern. Furthermore, Levy et al. (2012) show that local increased phytoplankton growth induced by vertical sub-mesoscale dynamics can be compensated by large scale effects on the thermocline and nutricline depths (e.g. nutrient vertical profiles) resulting from non linear scale interactions. In this case the phytoplankton production is in fact decreased in the sub polar gyre (due to shallower MLD and higher zooplankton grazing) and sub tropical gyres (due to deeper MLD and lower regenerated production). Shelf sea simulations that permit eddies are rare, and when they have been conducted tend to be of limited area and duration (e.g. Holt et al., 2004). While mesoscale eddies are commonly found in shelf seas (Badin et al., 2009), their role and prevalence is less clear in these regions than in the open ocean, particularly away from fronts. This arises from a limited observational base, particularly as remote sensed methods (altimetry and SST) are less effective in this case. Again computational restrictions prevent the routine use of eddy permitting/resolving resolutions and we must turn to subgridscale parameterisations, for example of submesoscale physics, in an attempt to represent these processes in both the open ocean and shelf sea contexts.

Beyond improved resolution and eddy processes, it is also necessary to realistically parameterise vertical mixing and the associated boundary layer dynamics (i.e. surface and benthic boundary layers and the pycnocline). For example, the timing and amplitude of the spring phytoplankton bloom, which is such a characteristic feature of the northern North Atlantic, is sensitive to wind in the late winter/early spring (Taylor et al., 2002). The largest blooms are seen under conditions of decreased storm intensity, which give rise to an early stratification of the water column and favourable light and nutrients for phytoplankton growth (Henson et al., 2006; Waniek, 2003). Accurate representation of synoptic scale atmospheric variability is required in order to simulate short-term variability in physics, which may help not only in predicting bloom dynamics but also other features such as realistic levels of primary production in the subtropical gyres (Popova et al., 2006) and the timing of the spring bloom in shelf seas. Alongside the forcing, the vertical mixing processes themselves must be accurately modelled, for example to accurately simulate production in the ‘deep chlorophyll maximum’. While there has been substantial progress in turbulence modelling (e.g. Umlauf and Burchard, 2005) accurately modelling mixing in strongly stratified condition

remains a challenge owing to its episodic (e.g. shear spiking) and non-local (e.g. Langmuir cells) nature.

A process that is particularly difficult to parameterisation, and yet critical in the northern North Atlantic, is deep convection. Deep convection shows strong inter annual variability (Dickson et al., 2003). It has been suggested that deep convection can sustain a viable phytoplankton population within the convective mixed layer during winter (Backhaus et al., 2003), a supposition that is supported by model studies (D’Asaro, 2008; Wehde et al., 2001) and observations (Pérez et al., 2005; Ward and Waniek, 2007). Even though the water column within the deep mixed layer is general homogeneous, the variable nature of deep convection can introduce heterogeneity on shorter timescales. While the retraction of the mixed layer between two periods of deep convective mixing may take days, primary production can react much more quickly and lead to small localised blooms in the absence of stratification, prior to the deep mixing re-homogenising the water column.

Process studies, using a 2D (vertical–horizontal) non-hydrostatic convection model coupled to a simple phytoplankton IBM have indicated that indeed low concentration of viable phytoplankton can be sustained in a convective regime with local short-lived growth events (Fig. 7). These process studies further indicated that, while the reduction in mixing depth towards spring leads to the expected increase in surface phytoplankton concentration, the mixed layer integrated biomass does not increase, as the higher concentration is compensated by the reduction in volume (Fig. 7). A comparable picture was found by Backhaus et al. (2003) at station M (66°N , 2°E), who measured winter chlorophyll in 1999 ($108 \text{ mg chl a m}^{-2}$) of the same order of magnitude to that of the spring bloom in 1997 ($130 \text{ mg chl a m}^{-2}$) (Irigoien et al., 1998). These findings point towards a potentially underestimated pool in the carbon budget that, being driven by submesoscale phenomena, is not well represent in basin-scale ecosystem models. To capture the winter phytoplankton dynamics and to improve the predictions of spring bloom onset, process-based parameterisations (related to turbulent mixing) rather than state-based (related to mixed layer depth) parameterisations could provide a way forward. In this context, net surface heat flux, commonly used to estimate conditions of deep convection, has consequentially been proposed to serve as a better indicator for phytoplankton growth conditions (Taylor and Ferrari, 2011) than the mixed layer depth.

Sensitivity of ecosystem dynamics to model physics may be particularly acute for complex models, e.g. those that incorporate multiple plankton function types (PFTs). Sinha et al. (2010) implemented one such model, PlankTOM5.2 (which includes mixed phytoplankton, diatoms and coccolithophores PFTs), separately into two 1° global GCMs, with identical ecosystem parameterisations and forcing in each case. Although globally integrated bulk properties, such as primary production and chlorophyll biomass, were similar, predicted distributions of individual PFTs varied markedly between the two simulations. Regarding the North Atlantic, relatively high mixing in one GCM led to dominance by diatoms, whereas a mixed phytoplankton community prevailed in the other GCM. The results highlighted that complicated models have more degrees of freedom, and so a greater variety of response to environmental conditions. A particular challenge then is how to assess the skill of the biogeochemical model independently of the physics. It is quite possible that inadequate physics is masking the skill of the biogeochemical models. One way forward is the retrospective analysis of large data sets to determine robust relationships between biogeochemical or ecological parameters, for example the robust empirical relationships between chlorophyll concentration and phytoplankton size classes (Brewin et al., 2010a; Hirata et al., 2011).

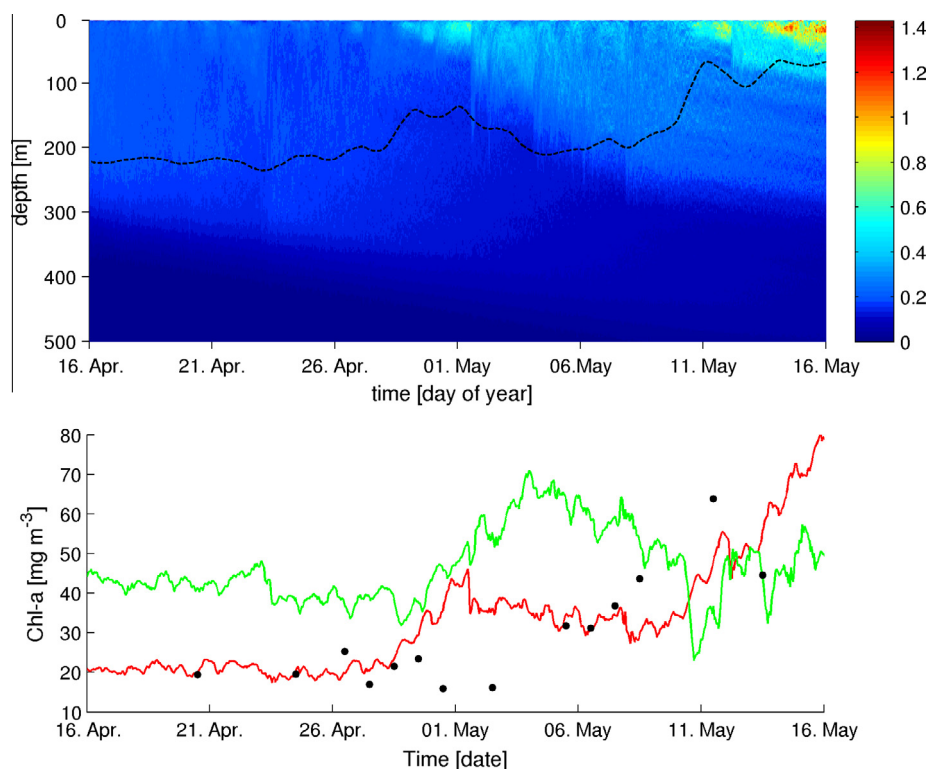


Fig. 7. Results from the 2D non-hydrostatic convection IBM model. Top: Profile timeseries of simulated chlorophyll concentration [mg chl m^{-3}] in 1997 at Station M. Black line indicates the mixed layer depth. Bottom: Chlorophyll concentrations over different integration depth: 100 m (red); mixed layer (green). Black dots show field measurements (100 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Phytoplankton

Phytoplankton lie at the heart of the marine biogeochemical system and the challenge of modelling such systems; they drive the transformation of C, N, P, Si and Fe from inorganic to organic forms, resulting in the decoupling of the carbon and nutrient cycles via heterotrophic biological activity and remineralisation processes. Changes in phytoplankton community composition alter the carbon (and nutrient) pathways through the food web. The community structure also dictates the magnitude of the vertical flux of organic material to the mesopelagic and benthos, its structure and stoichiometric composition. Consequently the inclusion of multiple phytoplankton PFTs such as diatoms, coccolithophores and picoplankton is an obvious choice for modelling the diversity associated with the North Atlantic ecosystem. Splitting phytoplankton between diatoms and non-diatoms is a common strategy. Diatoms dominate the spring bloom of northerly latitudes in the North Atlantic and can lead to substantial particle export that is transferred efficiently through the mesopelagic zone (Martin et al., 2011). This phytoplankton group also provides food for mesozooplankton, which are in turn linked to higher trophic levels such as fish. Fortunately for modellers, diatoms are the one phytoplankton type which is relatively straightforward to parameterise in models because, uniquely, they utilise silicate for growth. The characteristic spring diatom bloom in the North Atlantic has therefore been, by and large, successfully reproduced in biogeochemical GCMs and shelf seas models (e.g. Lewis et al., 2006; Yool et al., 2011). The details of amplitude, timing, and duration remain problematic to model as they are sensitive to the detailed juxtaposition of mixing and light.

However, matters are considerably less straightforward when it comes to accurately simulating other phytoplankton groups. A case

in point is the coccolithophores. Blooms of *Emiliania huxleyi* occur seasonally in the northern North Atlantic (Broerse et al., 2000; Holligan et al., 1993), appearing as milky seas on satellite images of ocean colour. These organisms flourish during high turbulence in the early stages of the spring succession, as well as during the stratified conditions that follow the spring bloom (Schiebel et al., 2011). Blooms of calcifying plankton (mainly Coccolithophores) can have significant impact on Total Alkalinity (Harlay et al., 2010) and air–sea fluxes (Shutler et al., 2012).

Using a parameterisation in which coccolithophores compete effectively at low nutrients, Le Quere et al. (2005) predicted coccolithophore blooms too far south in the North Atlantic. They concluded that an improved theoretical understanding is needed of the biogeochemical processes driving the growth and fate of PFTs in the ocean. Gregg and Casey (2007) used a global GCM to successfully reproduce coccolithophores distributions in the North Atlantic, although not in the North Pacific, where coccolithophores competed successfully with other phytoplankton when both nutrients and light levels were low. They concluded that “divergence among models and satellites is common for such an emerging field of research”. The coccolithophores example is illustrative of an ongoing tension in ecological modelling, namely the *a priori* requirement to increase complexity in order to achieve realism versus the need to acknowledge the unwelcome ramifications of complexity, which can impact the predictive skill of models. Difficulties include poorly understood ecology, lack of data, aggregating diversity within functional groups into meaningful state variables and constants, and sensitivity of output to the parameterisations in question and their physical and chemical environment (Anderson, 2005).

The computational cost of increasing biological complexity generally varies linearly with the number of state variables, compared

with the cubic increase associated with refining resolution. Hence this is a secondary consideration compared to whether there is a demonstrable improvement in predictive skill and also whether the overhead in making scientific interpretations of more complex models is acceptable. An increase in complexity would generally be considered worthwhile if accompanied by a demonstrable and unambiguous improvement in model skill. However, such demonstrations are elusive and there is, as yet, no consensus as to how many PFTs are required to represent key processes. Hence, flexibility in approach is needed in order to select appropriate levels of complexity, depending on the question, geographical area, and research agenda. This suggests the construction of model frameworks in which models of different complexity can be compared in a traceable fashion is highly desirable.

Zooplankton

Zooplankton play a pivotal role in the marine pelagic ecosystem, yet representing them in 3-D biogeochemical models (as distinct from the species specific or ecological models considered below) remains a major challenge (Carlotti and Poggiale, 2010). The most obvious division to make is between micro- and mesozooplankton, both groups being important in the North Atlantic. Microzooplankton may be responsible for consuming as much as half of the primary production in areas of the northern North Atlantic such as the Irminger Sea and the UK coastal waters and should therefore “be carefully parameterised in models of this region” (Burkill et al., 1987; Montagnes et al., 2010). Mesozooplankton, and especially copepods of the genus *Calanus*, are central to food web dynamics of the North Atlantic, impacting on both the biological carbon pump and transfer to higher trophic levels (e.g. Beaugrand, 2009; Beaugrand et al., 2003a). Given the enormous disparity between micro- and mesozooplankton in terms of rates of feeding, growth and reproduction, as well as in life history strategies, it is highly questionable whether, as in many NPZD models, they can be meaningfully aggregated into a single zooplankton state variable (e.g. Popova et al., 2006).

Many aspects of the parameterisation of zooplankton in biogeochemical models are in need of attention including functional response formulations to describe grazing (Gentleman et al., 2003), stoichiometric aspects of nutrition and trophic transfer (Hessen and Anderson, 2008), mortality terms (Ohman et al., 2004), and vertical migration with its potential impact on carbon export (Hernandez-Leon et al., 2001; Steinberg et al., 2002). One aspect of the zooplankton parameterisation that is of particular relevance to the North Atlantic is the formulation of nutrient excretion. When specified as a linear function of zooplankton biomass, (e.g. Aumont et al., 2003; Fasham et al., 1990), this may lead to unrealistically low rates of nutrient remineralisation via grazers. This problem is felt most acutely in the oligotrophic gyres in GCMs and, in conjunction with issues related to model physics (above), leads to extremely low predicted primary production in these areas. Significant improvement in the prediction of primary production can be made if excretion is instead described as a function of intake, rather than biomass (Baretta-Bekker et al., 1997; Oschlies et al., 2000; Popova et al., 2006). However, partitioning the excretion between DOM and POM remains a challenge. All in all, modelling zooplankton represents a major challenge for the future, especially in end to end models where these organisms are important both as consumers of primary production and as prey for higher trophic level organisms. While single life-stage models of zooplankton are probably adequate for biogeochemical cycling, this is not generally the case when coupling to higher trophic levels (Rose et al., 2010). In which case consideration multiple life stages is needed, and this is increasingly studied in detail using individual based models (IBMs); as is discussed below.

Key biogeochemical processes

One of the biggest challenges is the representation of the remineralisation processes in biogeochemical models specifically, the microbial loop including dissolved organic matter (DOM), remineralisation of export in the deep ocean, and benthic biogeochemistry in the shelf seas. The production and remineralisation of particle export production in the deep ocean is discussed in detail in (Sanders et al., this volume) so it not discussed here. The microbial loop is particularly important, especially in oligotrophic gyres and seasonally stratified shelf seas. It encompasses a range of, largely bacterially driven, processes, leading to the remineralisation of dissolved and particulate organic matter supplying nutrients to the euphotic zone to drive regenerated primary production. The dissolved component is by far the largest pool of organic matter in the sea. In the past DOM has been regarded as a large inert reservoir of carbon, which does not have a strong effect on the export flux of carbon and, below the oceans' mixed layer, is excluded from the present day carbon cycle. However, from the first fieldwork in the JGOFS program (Ducklow et al., 1995) studies have revealed that DOM is an active and highly dynamic component of carbon biogeochemical cycles and plays important roles in marine ecosystems (Carlson et al., 2010); its contribution to the total export towards the deep ocean can reach 20%.

However, modelling DOM has always been problematic because of the many processes associated with its production and fate, as well as the fact that it has varying composition and lability (Christian and Anderson, 2002; Goldberg et al., 2010). Currently there are three main types of representation of microbial loop processes in models. The simplest is the implicit remineralisation form, whereby POM is directly re-mineralised to bioavailable nutrients according to a prescribed rate (e.g. MEDUSA; Yool et al., 2011). The semi-implicit form includes those models that represent both DOM and POM, but bacteria are implicit in the DOM pool. For example, PISCES (Aumont et al., 2003) considers semi-labile DOM and particles of two size classes (distinguished by settling velocity). This model provides multiple pathways and hence time-scales for nutrient regeneration. Finally, the fully explicit model whereby bacteria is described along with POM and DOM, and bacteria are allow to compete with phytoplankton for nutrients (e.g. ERSEM; Polimene et al., 2006; Vichi et al., 2007). The choice microbial loop representation is function of the questions being asked by the models. Both MEDUSA and PISCES were designed to quantify the global ocean carbon cycle in both the global ocean and an earth systems modelling context, and thus require a relatively simple, computationally cheap representation. On the other hand if we wish to explore the ecological and biogeochemical consequences of microbial processes then we need to explicitly resolve bacteria in the model (e.g. ERSEM).

Several modelling studies (e.g. Anderson and Williams, 1998; Vallino, 2000) have suggested that inclusion of DON cycling can have important implications on the regulation of nutrient cycling. Salihoglu et al. (2008) showed that a missing bacteria component in the model can result in an important discrepancy between model and observations, specifically the simulated DON pool being too high during the period following the spring bloom, mainly due to the conversion of particulate organic matter to DON. Even the models that include bacteria compartments predict a strong annual DON cycle (Anderson and Pondaven, 2003; Hood et al., 2001; Spitz et al., 2001). This suggests that the remineralisation or the uptake kinetics of DON (or both) are not correctly represented and need to be re-evaluated as more observations become available.

Benthic processes and the resulting benthic–pelagic fluxes are highly significant in shelf seas. Modelling studies have calculated that benthic–pelagic fluxes of nitrogen and phosphorus contribute

to 33% and 35% respectively to the total nutrient budget on the northwest European Shelf and these compare well with observations (Proctor et al., 2003; and references therein). Many physical processes influence benthic–pelagic exchange. Particulate material, settling from the water column, can accumulate in an unconsolidated fluff layer, which is easily remobilised by bottom currents. Dissolved material is exchanged by diffusive processes in cohesive and non-cohesive sediments, whereas both dissolved and particulate material is exchanged by advective transport within non-cohesive sediments. All these processes are spatially dependent on sediment type and hydrodynamics (including surface waves), and affect the biogeochemical functioning of the benthic system. The extent to which they influence shelf-wide nutrient and carbon budgets is largely unknown. Currently there are two main approaches to modelling benthic processes. The first is a simple first order remineralisation of the detritus reaching the seabed to define a benthic nutrient flux. The second involves explicit models of benthic biota (Blackford, 1997; Ebenhoh et al., 1995) and benthic nutrient cycling, (Billen and Lancelot, 1988; Ruardij and Vanraaphorst, 1995), which have been developed for temperate European coastal waters. This has led to the development of coupled benthic–pelagic models, whereby the role of benthic nutrient cycling in controlling pelagic ecosystem dynamics can be explored (Allen et al., 2001; Holt et al., 2012a). From a modellers perspective the benthic system is severely under-sampled and the benthic models suffer from a basic lack of information on even the seasonal cycles of the ecology and biogeochemical processes. While this knowledge gap is beginning to be addressed, this is the major limitation to benthic model evaluation and future development.

Future developments in biogeochemical and LTL modelling

Modelling biogeochemical cycling in the ocean is a complex business and a number of other factors are important. The use of multiple currencies, and associated stoichiometry, is an ongoing topic for model development. Most biological models used in GCMs include a single macronutrient, usually N or P. The exception being the ERSEM family of models (Baretta-Bekker et al., 1997; Blackford et al., 2004; Vichi et al., 2007), which have multiple currencies (C, N, P, Si) and variable carbon and nutrient stoichiometry. The case for including both is for modelling either shelf seas or regions where there are anoxic zones, with associated denitrification; but the latter are not generally observed in the open ocean of the North Atlantic. Nevertheless it may be the case that, unlike in the South Atlantic, the North Atlantic subtropical gyre is depleted in phosphate, possibly as a result of nitrogen fixation enhanced by iron deposition in Saharan dust (Wu et al., 2000). Utilisation of dissolved organic phosphate then becomes an important source of nutrients for primary production in this area (Lomas et al., 2010; Mather et al., 2008). Aeolian dust fluxes have increased during the latter half of the 20th century and models predict that this trend may continue in future (Mahowald et al., 2005). The resulting stimulation of primary production may enhance the biological pump in iron-fertilised regions. However, matters are complicated in that, in order to reproduce biogeochemical feedbacks associated with aeolian dust, models should incorporate the contrasting effects of dust on different microbial groups, as well as associated competitive interactions with phytoplankton (Maranon et al., 2010).

Plankton is typically represented in models as belonging to one of two discrete trophic categories: autotrophic phytoplankton or heterotrophic zooplankton. However, the mixotrophs that are found in all aquatic environments (Stoecker, 1998), and play an important role in determining ecological and biogeochemical dynamics, are generally disregarded in ecosystem models. Zubkov and GA (1998) found that the photosynthetic phytoplankton

accounting for more than 80% of the total chlorophyll in regions of the North Atlantic, were also responsible for 40–95% of the total grazing upon bacteria. These results may have profound implications for our understanding of carbon and nutrient cycling in the North Atlantic and provide a major challenge for future model development.

An ever present concern of ecosystem studies (not least modelling) is the availability of an appropriate observation base. However, in addition to scientific cruises and moorings, the last two decades have seen the emergence of new techniques, such as ocean colour satellite sensors and ARGO floats (some of them equipped with oxygen sensors), which providing a continuous monitoring of key biogeochemical variables, and thus opens the possibility of assimilative approach to ecosystem modelling (Brasseur et al., 2009; Ciavatta et al., 2011).

Finally, we should take note of a comment made by the great marine ecosystem modelling pioneer Gordon Riley 60 years ago, that a “thorough knowledge of the physiology and ecology of particular species and ecological groups” is a prerequisite for effective ecosystem models, (Riley, 1952). Although our understanding of the competitive interactions of PFTs, as mediated by environment, is improving (e.g. Feng et al., 2009), the extent to which we are in a position to formulate parameterisations for reliable prediction based on this knowledge remains an open question.

Lower trophic level modelling in EURO-BASIN

A fundamental challenge, arising from the issues discussed above, is to find the appropriate level of complexity that will enable ecosystem models to have optimal skill in simulating and predicting biogeochemical fluxes, and also providing appropriate and accurate fields for coupling to HTL models. The ideal level of ecosystem complexity to study ocean biogeochemical processes is an ongoing debate, and as a result many contrasting models are used in the North Atlantic. These models differ not only in their structure, but also in their formulation and the parameterisation of key processes, such as phytoplankton growth, trophic transfer and export of organic matter to the deep ocean. Although diversity in approach can be desirable, a coordinated strategy for comparing models of different complexity should help improve the models, help identify key uncertainties, and ensure compatibility with parallel efforts (e.g. in shelf seas modelling).

To try and untangle these problems, a traceable hierarchy of models is a useful concept to consider and this is the approach we adopt in EURO-BASIN. We use NEMO as the general circulation model, with common forcing to harmonise the physical environment for the various ecosystem models and so facilitate the analysis and inter-comparison. Following this approach we will make an ensemble of simulations using a range of simple and more complex ecosystem models. This will allow us to build up a multi-model, multi-scenario ‘super-ensemble’. To describe the planktonic ecosystem we have chosen to compare intermediate complexity (PISCES, MEDUSA) with a more complex plankton functional type (ERSEM) model (Fig. 8).

PISCES (Pelagic Interaction Scheme for Carbon and Ecosystem Studies; Aumont et al., 2003) considers two phytoplankton (with 4 co-limiting nutrients: N/P/Si/Fe) and two zooplankton, with an explicit semi labile DOM and two particle sizes. Using N as the main currency, as well as P, Si and Fe, it also simulates the C (DIC and alkalinity) and O cycles. The meso pelagic model takes into account particle dynamics between the two sizes, and exchanges between particles, DOM and inorganic pools.

MEDUSA (Model of Ecosystem Dynamics, nutrient Utilisation and Sequestration; Yool et al., 2011) is a modestly complex ecosystem model, it includes two phytoplankton, two zooplankton and

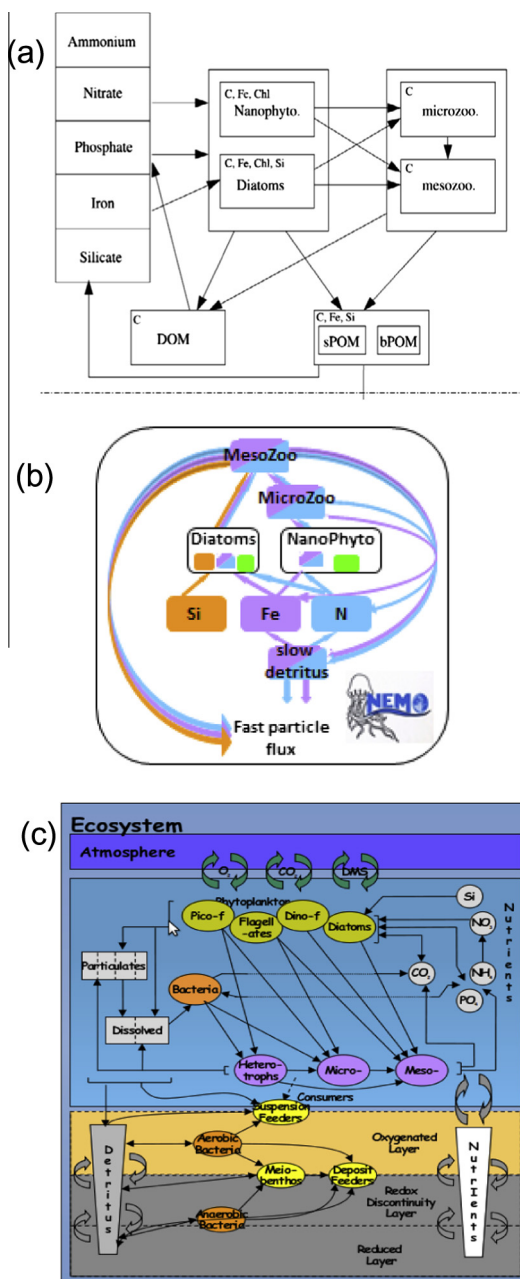


Fig. 8. Schematics of the three LTL models included in EURO-BASIN: (a) PISCES; (b) MEDUSA; (c) ERSEM.

three nutrients, and is specifically designed for open ocean applications.

ERSEM (European Regional Seas Ecosystem Model; Baretta et al., 1995) was developed as a generic lower-trophic level/biogeochemical cycling model. ERSEM is an intermediate/high complexity model originally designed for simulating shelf seas biogeochemistry and ecosystem function. ERSEM simultaneously describes pelagic and benthic ecosystems in terms of phytoplankton, bacteria, zooplankton, zoobenthos, and the biogeochemical cycling of C, N, P, Si.

By running these different models in the same physical environment we can begin to quantify structural and parameter uncertainty. This diversity of models is required for two reasons. First they extend the range of scenarios and therefore give a constraint on the combined parameter and structural uncertainty. Second, and perhaps more importantly as we are still learning how to

Table 2
Summary of the model runs shown in Figs. 8–10.

Model	NEMO configuration	Atmospheric Forcing	References
MEDUSA	1° Global	ERA 40	Yool et al. (2011)
PISCES	1/2° Global	DFS4	Aumont et al. (2003)
ERSEM	1° Global	ERA 40	Blackford et al. (2004)

model these processes, they inform future model development through the comparison of approaches with an in-depth analysis of the biogeochemical fluxes involved and through validation against available *in situ* and remote sensing data.

Here, we illustrate the approach using existing model simulations and compare results from three global applications of these three LTL models. Each exists within a similar, but not identical physical framework (e.g. some differences in resolution and atmospheric forcing; Table 2), so we limit our discussion here to a qualitative assessment. Fig. 9 shows a meridional (N–S) surface chlorophyll transect of the North Atlantic for all three models and SeaWiFS ocean colour based chlorophyll. In all cases, between 25°N and 50°N the models reproduce the spatial trends and concentrations of chlorophyll quite well, but underestimate the chlorophyll concentrations south of 25°N. The largest differences between the models occur north of 50°N; an explanation for this has yet to be established. Fig. 10 shows a comparison of annual mean surface chlorophyll and phytoplankton community structure for the three models in terms of diatoms and non-diatoms for the period 1998–2004 for the three models. In addition we also show the equivalent satellite phytoplankton community structure data product derived from SeaWiFS (Brewin et al., 2010b; Hirata et al., 2011).

All the models produce the general observed north–south trend in chlorophyll concentration and diatom distribution, with both chlorophyll and diatoms dominating in the north of the domain (Figs. 9 and 10). This suggests to a first order the emergent property of this simple community structure functions well in all three models. However, the modelled diatom fraction appears overestimated in all three models compared with the satellite product. The question remains whether or not these discrepancies are a function of the physical model, the biogeochemical models or some combination of both, alongside observational uncertainty.

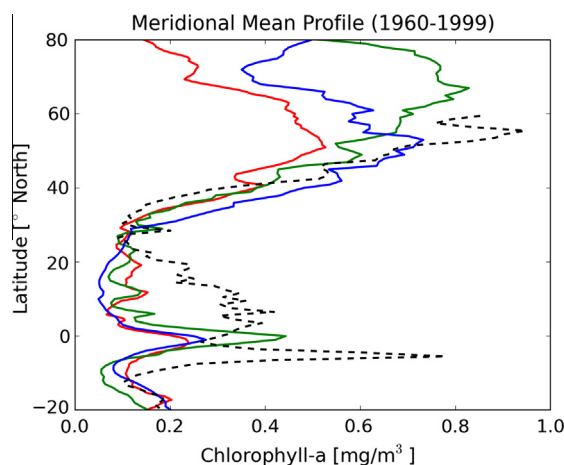


Fig. 9. Meridional transect through the N Atlantic comparing the outputs of SeaWiFS (dotted) with the EURO-BASIN models PISCES (green), MEDUSA (red) and ERSEM (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

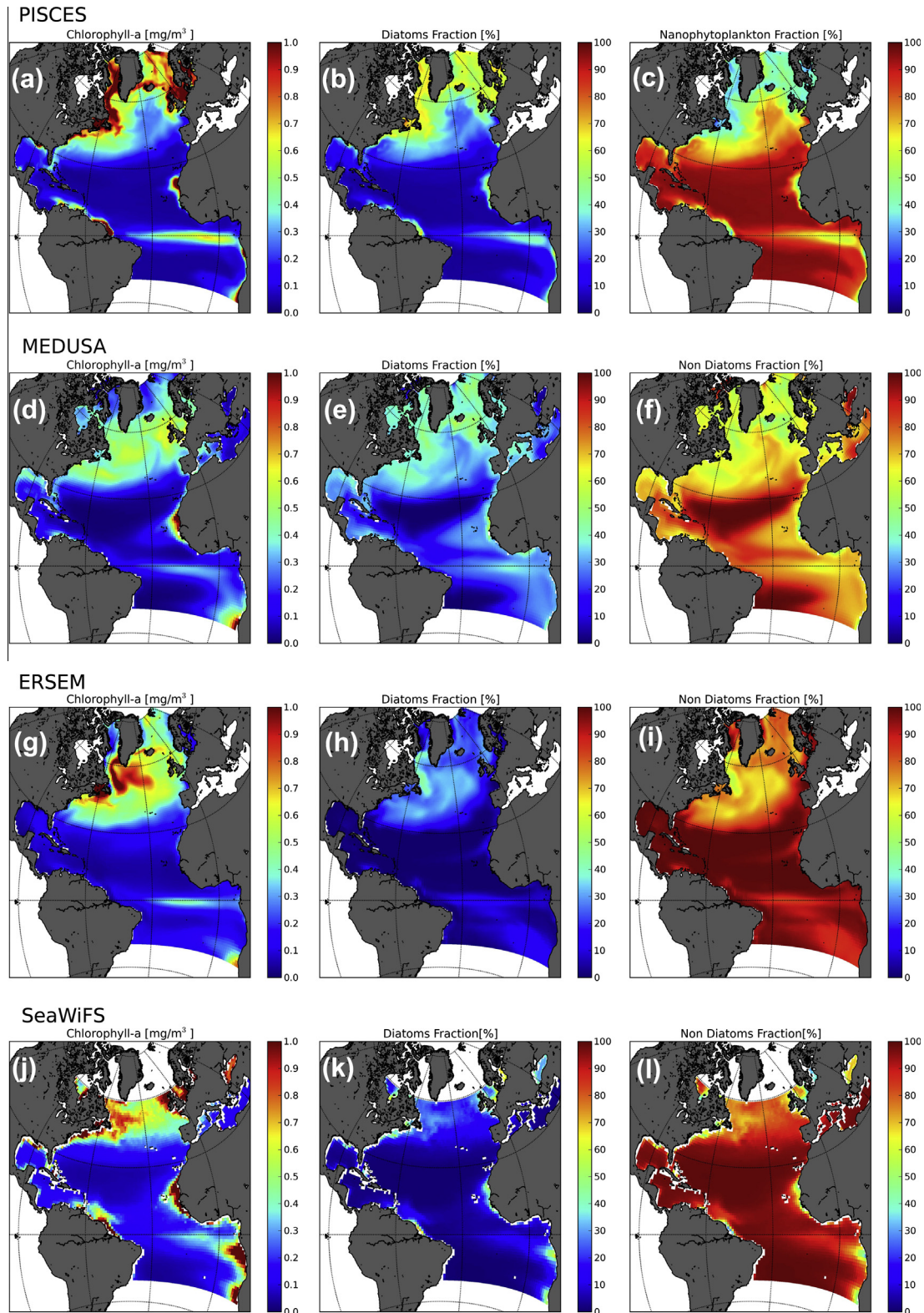


Fig. 10. Annual mean sea surface chlorophyll (mg m^{-3}), percentage fraction of diatoms and percentage fraction of non-diatoms (1998–2004), for PISCES (a, b, c), MEDUSA (d, e, f), ERSEM (g, h, i) along with estimates from the SeaWiFS satellite (Hirata et al., 2011 j, k, l). See Table 2.

The impact of the coarse scale physics is apparent in all the simulations, an aspect that will be specifically addressed in EURO-BASIN. The satellite chlorophyll clearly shows that the high chlorophyll concentrations in the North Atlantic lie to the north of the Gulf Stream. In the models the high chlorophyll extends further

south, showing a much more diffuse boundary with the subtropical gyre, which in turn is too far south in all the models. This is most likely due to the poor representation of mesoscale physics on the northern boundary of the gyre and highlights a major challenge: that of disentangling the performance of the biogeochemical

model from that of the physics. It may be in many cases that the performance of the biogeochemical models is masked by that of the physics. There is a need for metrics that assess the fidelity of the biogeochemical processes independently of the physics, which points to the role of meta-analysis to define robust testable global relationships between biogeochemical variables.

To illustrate this point we draw on a meta-analysis of over 3000 observations of collocated HPLC chlorophyll and accessory pigment data, which shows that there is a robust empirical relationship between chlorophyll concentration and the fraction of diatoms in the community (Hirata et al., 2011). Diatoms dominate at chlorophyll concentrations above 1 mg chl m^{-3} . Fig. 11 shows density plots illustrating the relationship between chlorophyll and the % diatom fraction for all three models, and SeaWiFS as a reference. In all cases the models capture the observed response of increasing diatom fraction with increasing chlorophyll concentration; however MEDUSA and PISCES systematically over-estimate the diatom fraction. The crucial point is not the performance of the respective models per se, but the fact that we can see a general response of the plankton models (in this case an emergent relation between community and chlorophyll) that is independent of the hydrodynamic model.

Higher trophic levels modelling: state of the art, challenges and gaps

Alongside models focusing on biogeochemistry and LTLs, such as those considered above, are models that aim to capture other aspects of the ecosystem in some detail. Examples include models

that represent foodwebs, species behaviour and interaction, and the structure and function of the whole ecosystem. As with physical models, the different characteristics and questions relevant to open ocean and coastal ecosystems have led to a diversity of modelling approaches that is still growing rapidly. Moreover, due to the societal and economical value of many exploited living marine resources, a substantial effort has been devoted over the last decades to the development of specific population models for the management of fisheries. In the open ocean, the focus is on large pelagic and highly migrant species, like tunas and billfishes, which feed opportunistically on a large range of micronektonic forage species (size $\sim 1\text{--}20 \text{ cm}$). In shelf seas, exploited species include bottom (e.g., plaice, halibut), demersal (e.g., cod, hake) and small to medium size pelagic species (e.g., herring, mackerel blue whiting, sardines, anchovies). These feed on benthic organisms as well as zooplankton.

Past food web studies have tended to treat the upper and lower trophic levels separately; the use of detailed simulations of physical dynamics requires some limitation on biology. This led de Young et al. (2004) to propose that “rather than model the entire ecosystem we should focus on key target species and develop species-centric models”. The focus of benthos and the upper trophic level studies is often on predatory interactions based on fish diet data (Garrison and Link, 2000; Heath, 2005). Linear, steady-state, food-web models have been used to represent these complex interactions (Pauly and Christensen, 1993). This trophic-centric approach does not include the dynamics of individual species and neglects the physical processes. Steele and Gifford (2010) argue that these two sets of simplifying assumptions are

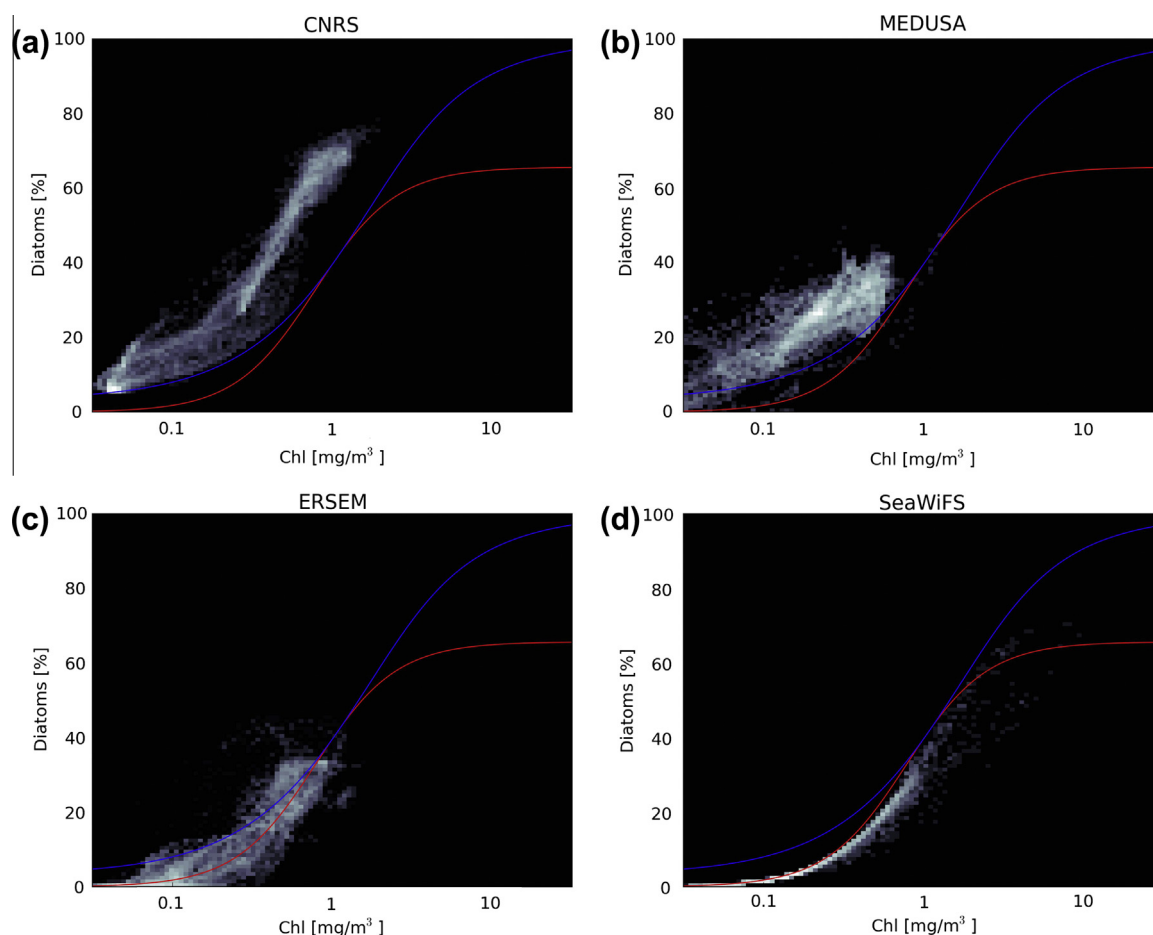


Fig. 11. Density plots of diatom fraction (%) against \log_{10} chlorophyll for (a) PISCES, (b) MEDUSA, (c) ERSEM, (d) SeaWiFS.

complementary and answer different questions about the dynamics of individual populations and the productivity of ecosystems.

Recently, in response to the desire to move towards an ecosystem-based approach to marine management, end-to-end models representing the entire trophic structure and physical components of the ecosystem at a fine spatial scale have been developed (Cury et al., 2008; Rose et al., 2010). One approach is to combine aggregated versions of existing food web models of the upper trophic levels, with NPZD formulations of the microbial web, and with simplified representations of the main physical forcing (e.g. Kearney et al., 2012; Steele et al., 2007; Steele and Ruzicka, 2011). The critical issue is whether the use of functionally defined groups or guilds, rather than species, as variables, can achieve portability, while retaining adequate realism.

The small pelagic species group in particular is strongly dependent on the abundance of a few copepod species (*Calanus* spp.) that dominate the mesozooplankton in the North Atlantic Basin. This motivates the development of specific models to study the complex life histories of these zooplankton species.

Copepods

Copepods have several developmental stages from eggs through nauplii and copepodites to adults, as well as a diapause stage, in deep water over winter. Marked differences exist between species. For example, copepods that inhabit the North Pacific are relatively large and have a single generation per year, as compared to the smaller copepods in the North Atlantic, which undergo several generations per year (Parsons and Lalli, 1988). A complicating factor in the North Atlantic is that there are two dominant species: *Calanus finmarchicus* and *Calanus helgolandicus*, with distinct niches. The former is adapted to the colder temperatures of the northwest North Atlantic, in contrast to *Calanus helgolandicus* which prefers warmer temperatures and dominate further south and east (Helaouet and Beaugrand, 2007). Changes in temperature, for example due to climate change and variability, could therefore significantly impact on the distribution of these two species (Møller et al., 2012), with potential impacts on the recruitment of Atlantic cod (Beaugrand et al., 2003a).

A number of copepod population models have been developed that target the distributions and production of key species. For example, Carlotti and Radach (1996) studied the seasonal dynamics of *Calanus finmarchicus* in the North Sea using a one-dimensional water column model. Heath et al. (1997) used a Lagrangian 1D approach, using output from a 3-D hydrodynamic model, to study the dynamics of *Calanus* in the Fair Isle channel (northern North Sea). Three-dimensional approaches have also been adopted, for example, Bryant et al.'s (1997) study of the seasonal dynamics of *Calanus finmarchicus* in the northern North Sea and Stegert et al.'s (2009) study of the population dynamics of *Pseudocalanus elongatus* in the German Bight (North Sea). Regarding the North Atlantic, a major modelling study was undertaken by Spiers et al. (2005, 2006), examining the distribution and demography of *Calanus finmarchicus*. The model followed progression from eggs through six naupliar stages, five copepodite stages and adults. An interesting aspect of the study is that it explored the mechanisms controlling diapause, suggesting that irradiance may be an important queue for both the onset of, and awakening from, diapause (Spiers et al., 2005). However, the application of population-based models, which represent life history in terms of age and developmental stage of body weight, within biogeochemical models is problematic (Carlotti and Poggiale, 2010). There are substantial technical challenges and computational requirements associated with highly resolved population models in 3-D. At a more fundamental level, a significant challenge in modelling species such as *Calanus finmarchicus* is that many aspects of its biology

are poorly understood (Spiers et al., 2006). The mechanisms involved with diapause provide one good example.

Individual Based Models (IBMs) keep track of each individual in a population, in a primarily Lagrangian framework (DeAngelis et al., 1979; DeAngelis and Gross, 1992; Grimm and Railsback, 2005). In these models individuals can be characterised by state variables such as weight, age and length, and they may also allow behavioural strategies to be implemented in a spatial context. This allows the properties of a population to be described by the properties of its constituent individuals. Model validations against data can be done at the individual level; matching the observational approach. Moreover, models based on individuals benefit from having the same basic unit as natural selection. This makes IBMs appealing for addressing behavioural and life history tradeoffs and therefore for studying higher trophic levels, which can have a great behavioural repertoire, in particular in relation to motility. Consequently individual based modelling is used extensively for modelling higher trophic levels in EURO-BASIN. There have been several applications of IBMs to zooplankton in the North Atlantic. Early studies focused on simulating drift trajectories of individual plankton and their growth, survival and reproduction (Carlotti and Wolf, 1998; Miller et al., 1998). Models have subsequently been fitted with adaptive traits in order to investigate the consequences for adaptation and population dynamics of different levels of environmental forcing (Fiksen, 2000; Huse, 2005). More recently there have been applications using super-individuals that allow entire populations of zooplankton to be simulated with an individual based representation (Hjøllo et al., 2012).

Open ocean Mid-Trophic Levels (MTL)

For basin or global scale modelling, an exhaustive representation of all mid-trophic level species is unrealistic and unnecessary. It is more appropriate to consider a hybrid approach combining functional groups of forage species (e.g., mesopelagic fish) and specific detailed population submodels for a few species of interest (herring sardines, etc.). On the top of this the approach should also consider the large oceanic predator species, fisheries and associated fishing mortality. Ideally, in such an integrated approach, each functional group would include specific population model representations, either based on Lagrangian (IBM) or Eulerian approaches. While this vision may appear ambitious and technically challenging, the level of computation can be drastically reduced for these specific population submodels, using a 2D or layer-based 3D approach, and degrading the spatial resolution of the physical model. Key components of this integrated approach for MTL modelling already exist or are the subject of ongoing developments. Moreover, there are examples of modelling approaches of MTL functional groups that have been developed to link lower biogeochemical models to population dynamics of large oceanic predators that can be drawn upon.

One such approach proposes a representation of basin-scale spatiotemporal dynamics of six functional groups of MTLs (Lehodey et al., 2010), here applied to the North Atlantic. The definition of these groups is based on the occurrence or absence of diel migration between the surface (epipelagic), subsurface (mesopelagic) and deep (bathypelagic) layers (Fig. 12). Their dynamics are driven by temperature, currents, primary production and euphotic depth simulated by a coupled physical–biogeochemical model. The vertical structure is currently a simplified 3-layer ocean, and to obtain the biomass during the day and night in each layer, the components are summed according to their day and night position (Fig. 12). Recruitment, ageing, mortality and passive transport by horizontal currents are modelled within an Eulerian framework, taking into account the vertical migration of organisms. The temporal dynamics are based on a relationship linking

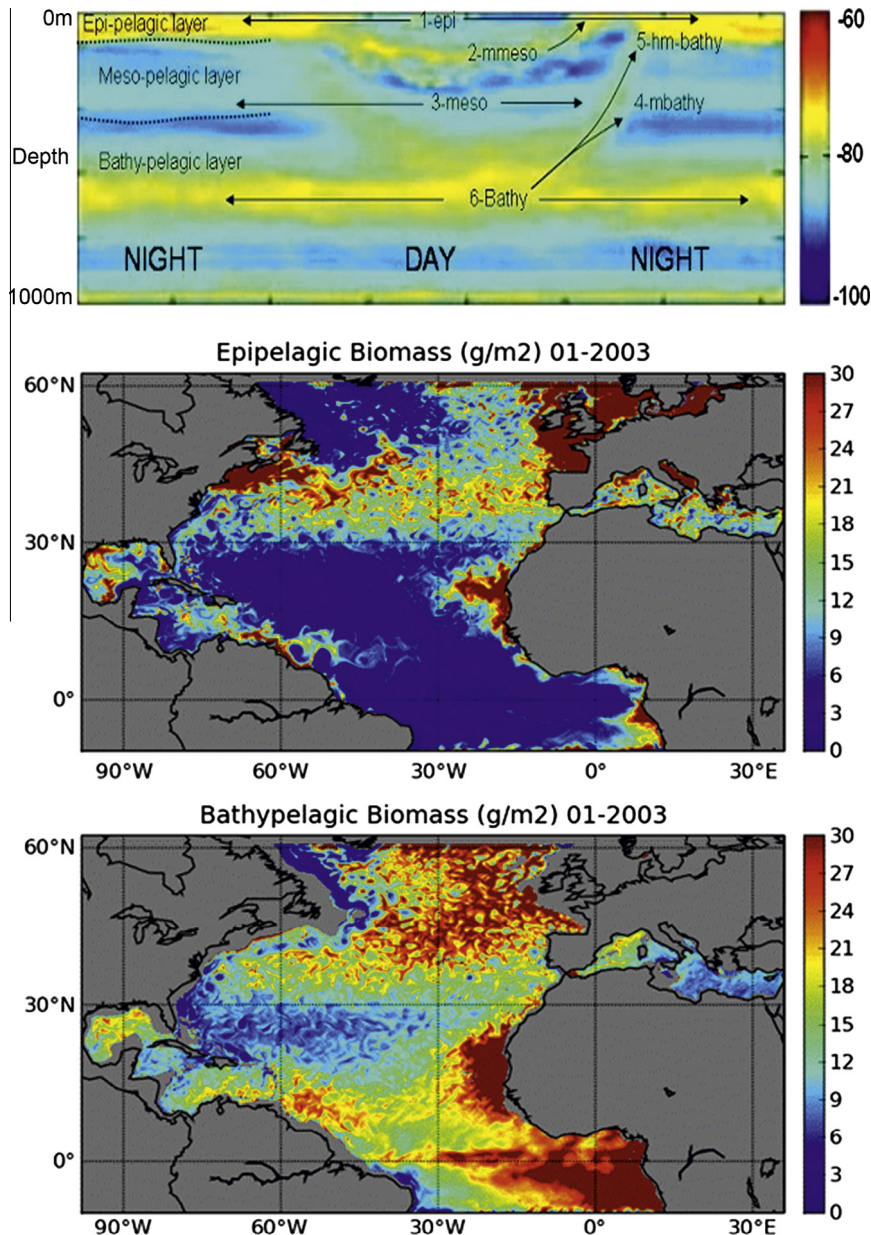


Fig. 12. Mid-trophic functional groups. Top: echogram showing monthly average (November 2004) diurnal variation from the stationary lander located at the Mid Atlantic Ridge (MarEco Project; kindly from Nils Olav Handegard, IMR, Norway) with identified MTL groups (m- for migrant, hm- for highly-migrant), according to Lehodey et al. (2010). Middle and bottom: comparison between predicted biomass of epipelagic and bathypelagic mid-trophic functional groups at a resolution $1/12^\circ$.

temperature and the time of development of MTL organisms, using macroecological principles that define the energy transfer through the biomass size spectrum (Brown et al., 2004; Dickie, 1976; Jennings et al., 2002; Kerr, 1974). Since the dynamics are represented by this well established relationship, there are only six parameters in the model that need to be estimated. The first defines the total energy transfer between primary production and all the MTL groups, while the others are relative coefficients, redistributing this energy through the different components. A notable advantage of this simplified approach is that it facilitates the optimisation of parameters through the assimilation of acoustic data. In particular, the matrix of size distribution coefficients can be straightforwardly estimated using relative day and night values of acoustic backscatter, integrated in each of the three vertical layers of the model. This facilitates the use of different un-standardised acoustic profiles (Handegard et al., 2013) in constraining the model.

Small pelagic fish

Models simulating the drift of fish eggs and larvae using Lagrangian approaches have become commonplace in the last few decades, but there are still rather few comparable models for adult fish. The added complexity of addressing the greater behavioural repertoire of adult fish adds challenges to the modelling. With regards to the North Atlantic, models have been developed for the Barents Sea capelin (*Mallotus villosus*), where the focus has been on simulating the movement from first principles (Huse, 2001); relatively few IBMs focus on simulating the entire life cycle of fish stocks. Initial attempts were made in this to study the Barents Sea capelin (Huse, 1998; Huse and Ellingsen, 2008), which illustrated the flexibility of the individual based approach in coupling movement, behaviour with growth, survival and eventually recruitment under different climate scenarios (Huse and Ellingsen, 2008).

Large oceanic species

The distribution of micronekton is a prerequisite for modelling the spatial dynamics of their predators, i.e., the large pelagic species such as tuna and swordfish. The Spatial Ecosystem and Population Dynamics Model (SEAPODYM) uses this distribution to simulate the full life cycle of the large pelagic species from eggs to oldest adults (Lehodey et al., 2008). The SEAPODYM model includes: a definition of spawning, local movements as the responses to habitat quality and also through basin-scale seasonal migrations, accessibility of forage for fish within different vertical layers, predation and senescence mortality and its change due to environmental conditions. Data assimilation techniques, based on an adjoint method and a maximum likelihood approach, are implemented to assist the parameterisation using historical fishing data (Senina et al., 2008).

In the North Atlantic basin, albacore tuna (*Thunnus alalunga*) has been one of the most exploited pelagic species (Arrizabalaga et al., 2004), and shows a major and steady declining trend during the last 40 years. It is unclear if this decline is due to overfishing, shift of fisheries to other target species or changes in environmental conditions (e.g. climate change and variability). The preliminary application of SEAPODYM model to this species suggests that the environment has been a strong driver in the observed trend of the last decades (Fig. 13). In particular, the model predicts changes in biomass of micronekton in the tropical region that are linked to changes in temperature predicted by the ocean GCM (NEMO-ORCA2 forced by NCEP reanalysis); this still needs to be validated with observations.

Trophic cascades and two way coupling

The example of Atlantic albacore tuna suggests a combined effect of fishing and bottom-up forcing; these are usually thought to be the main forcing in the open-ocean systems (Steele, 1998). Top-down effects, or trophic cascades (Pace et al., 1999), have as yet only been detected in the ecosystems of some shelf and enclosed seas, for example, the Black Sea (Daskalov et al., 2007), the Baltic Sea (Casini et al., 2008; Mollmann et al., 2008) and parts of the shelf seas of the Northwest Atlantic (Frank et al., 2005; Frank et al., 2006; Myers et al., 2007). But there are now strong indications of top down control from planktivorous fish on zooplankton in the Norwegian Sea (Huse et al., 2012). This suggests that top down control can be important for basin scale ocean areas as well. Trophic cascades occur when the abundance of a top predator is decreased, releasing the trophic level below from predation. The released trophic level reacts by an increase in abundance, which imposes an increased predation pressure on the next lower trophic level, and so on. The occurrence of trophic cascades is dependent on temperature (high temperature leads to faster growth rates and therefore less sensitivity to fishing) and diversity (higher diversity stabilises the system; Ciannelli et al., 2005; Frank et al., 2007). Frank et al. (2007) stated that cold and species-poor areas such as the North Atlantic might readily succumb to structuring by top-down control and recover slowly (if ever). In contrast, warmer areas with more species might oscillate between top-down and bottom-up control, depending on exploitation rates and, possibly, changing temperature regimes. Nevertheless, the heavily exploited North Sea seems not to show any sign of trophic cascade (Reid et al., 2000).

Different approaches are necessary to investigate and model the two-way coupling between lower and upper trophic levels within their physical and chemical environment. As noted above, the shelf seas of the northern Atlantic Basin are dominated by small pelagic species (e.g., herring, sardines, anchovy, capelin), for which the coupling should occur at the zooplankton level that provides the

bulk of prey biomass to small pelagics. Then, sensitivity analyses simulating changes in fishing mortality of these commercial species can help explore the top down effect of these changes. However, there is often a group of a few species that share the same ecosystem, with their abundance fluctuating according to their own dynamics and in response to environmental variability and top-down factors (fishing or predation). Thus, multi-species models of small pelagic populations appear to be necessary to achieve a minimum degree of realism.

For the basin scale pelagic system, where exploited species are at a higher trophic level (tuna, swordfish), a first necessary step would be to shift the closure term in the LTL model to the next trophic level, i.e. to MTLs. These new functional groups can be coupled to zooplankton and POC model variables directly through predation and mortality rates. However, since this parameterisation is very challenging, an alternative would be to use the spatio-temporal dynamics of MTL groups, as already simulated above, to introduce relative variability around the average parameters of zooplankton mortality and POC production that are already estimated in current biogeochemical models. For example, a high (low) biomass of MTL would be translated through an increase (decrease) of the average mortality coefficient of zooplankton, in a given range that guarantees the numerical stability of the simulation. From this extension of ocean ecosystem models to MTL functional groups, a first expected result would be a better representation of zooplankton grazing, integrating spatial and temporal shifts in grazing pressure due to the dynamics of MTL organisms themselves. In addition, a better dynamical representation of processes in detritus uptake and release by meso- and bathy pelagic organisms might be expected.

Beyond this, spatial population dynamics models of large marine predator species and their fisheries would need to be coupled to MTL components through their predation on these groups. Here also the parameterisation of predation rates is challenging, especially if not all the predators species are included in the model. However, as with the coupling between MTL and LTL, a similar alternative could be to work, at least in a first instance, in terms of relative variability that does not prevent the exploration of the propagation of the top-down signal due to fishing pressure to the lowest trophic level.

Higher trophic level modelling in BASIN

Modelling the top-down effects of fishing on oceanic mid-trophic and lower trophic levels requires not only the two-way coupling of these different components of the ecosystem, but first and foremost the correct quantitative estimate of biomass and spatial dynamics of higher trophic levels under the influence of both environmental variability and fishing impacts. Unfortunately, despite a large effort to develop quantitative approaches for stock assessment over the past 50 years, a large uncertainty remains on many exploited stocks concerning their total biomass and their spatio-temporal dynamics. There is still a long way to go to reconcile the recent progress achieved in physical and biogeochemical/LTL oceanography on the one hand and marine ecology, focusing on spatial dynamics and population dynamics on quantitative estimate of change of abundance in time, on the other hand. The Euro-Basin project is a strong pluridisciplinary effort towards this goal. Below we summarise the key higher trophic level models applied in the EURO-BASIN project.

NORWECOM (IBM) The Norwegian Ecological model system NORWECOM (Aksnes et al., 1995; Skogen et al., 2007) was originally a biogeochemical model system with two functional groups: diatoms and flagellates. This model has recently been coupled to an IBM for the copepod *Calanus finmarchicus* (Hjøllo et al., 2012) and the planktivorous fish stock Norwegian spring spawning herring,

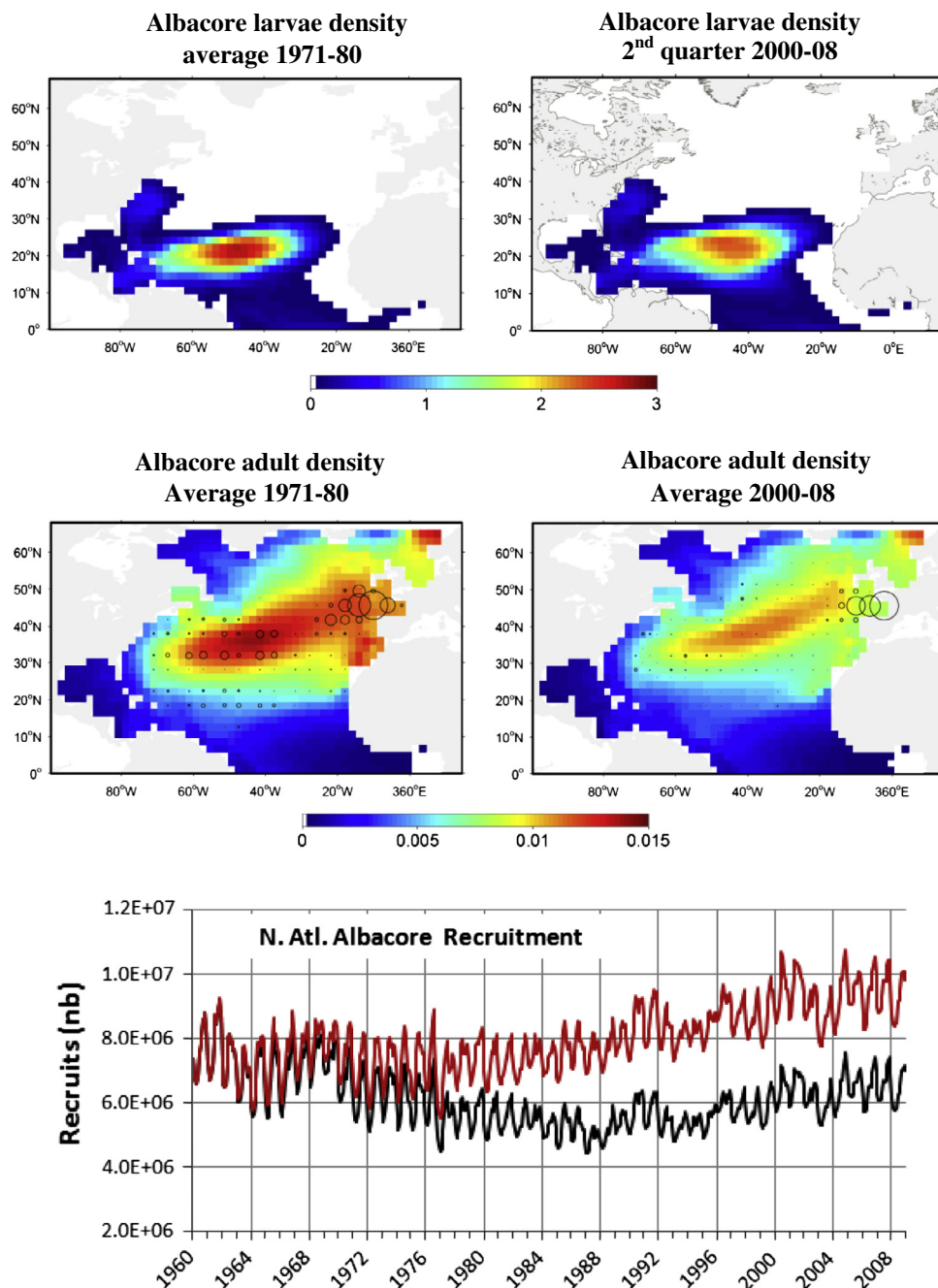


Fig. 13. The first SEAPODYM application to North Atlantic Albacore tuna. The maps show an average decadal distribution of albacore larvae (Nb. km⁻²) and adult (metric t km⁻²) density during first and last decade of the series, with total catch proportional to circle size superimposed on adult distribution. The bottom plot compares the time series of predicted albacore recruitment from the model SEAPODYM with (black curve) and without (red curve) fishing impact. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

blue whiting and mackerel (Utne et al., 2012). These developments are part of an ongoing plan to develop this into NORWECOM.E2E, or a full end-to-end model system. This model system has recently been applied to simulate the interactions between fish stocks in the Norwegian Sea and their utilisation of common zooplankton resources (Huse et al., 2012). Within EURO-BASIN, NORWECOM will be used to address the trophic couplings in the Norwegian Sea and the Calanus component will be integrated with NEMO and ERSEM to study Calanus dynamics within its entire distributional range.

APECOSM The Apex Predators ECOSystem Model (Maury et al., 2007a, 2007b) is a spatially explicit size based model of open ocean

ecosystems, based on a Dynamic Energy Budget approach. It is two-way coupled to the PISCES ecosystem model which in turn is coupled to the 1/4° NEMO North Atlantic physical model. APECOSM's philosophy is to specify a very generic and robust structure of marine ecosystems from which particular regional ecosystem organisation emerges due to interactions with the environment. It relies on a very few general rules from which the structure of the model and the parameterisations are derived mechanistically. APECOSM represents the flow of energy through the ecosystem with a size-resolved structure horizontally and with time. The uptake and use of energy for growth, maintenance and reproduction by the organisms are modelled according to the DEB (dynamic

energy budget) theory (Kooijmann, 2000) and the size-structured nature of predation is explicit. Distinction between the epipelagic community, the mesopelagic community and the migratory community that experiences nyctemeral vertical movements and hence transfers energy between the two other communities is also expressed; their habitat depends mainly on the light profile. Thus, size and spatiotemporal co-occurrence of organisms structure trophic interactions.

SEAPODYM-MTL (MTL) Spatial Ecosystem and Population Dynamics Model-Mid-Trophic Levels (Lehodey et al., 2010). As already described above in more detail, this is a three-layer bulk biomass functional type pelagic-ecosystem model combining energetic and functional approaches based on the vertical behaviour of organisms and following a temperature-linked time development relationship.

How these models are brought together with the physical and LTL models is summarised in Section 'Concluding remarks: integrating the EURO-BASIN models'.

Climate change projections for marine ecosystems of the North Atlantic

In order to define the envelope of response to climate change of marine ecosystem function, we must establish a range of scenarios that encompass possible future conditions that are scientifically and societally plausible. Coupled atmosphere–ocean general circulation models (AO–GCMs) provide the best available source of information for this purpose on a global scale, but this information is generally on too coarse a grid scale to be relevant for many regional scale studies, and so limits the application of the models. Moreover, even on a basin scale, mesoscale activity makes up a crucial component of the dynamics of the North Atlantic, and hence potential changes to its physics; this activity is absent in the majority of the ocean components of the current generation of AO–GCMs. Similarly shelf sea processes (e.g. tides and coastal currents) are not generally represented. Hence, a downscaling procedure is required: the AO–GCM is used to provide boundary conditions (surface and in some cases lateral) for EURO-BASIN models of finer resolution and more appropriate process representation.

Alongside the choice of AO–GCM forcing are two important considerations: the emissions scenario(s) and the forecast horizon. The emissions scenarios prescribe the atmospheric concentrations of radiatively active constituents, which in turn determine the radiative forcing of the AO–GCM. These are either derived from a socio-economic 'story-line' or prescribed to specific values (RCP's). The forecast horizon dictates how far into the future the model simulations will be conducted. The crucial issue here in climate change studies is whether a significant signal can be detected against the background of natural variability. This is a crucial factor for the North Atlantic, where this variability is exceptionally large.

The uncertainty in future projections can then be thought of as being a combination a three factors: scenario uncertainty (reflecting the unknown future socio-economic landscape), model uncertainty (reflecting inaccuracies in the model; this can be characterised to some extent by comparing different modelling approaches) and internal variability (reflecting the difficulty in detecting a clear climate change signal until this 'averages out'). This is well illustrated, in the global context, by the work of Hawkins and Sutton (2009), which shows how model and "internal variability" uncertainty decrease with lead time, but scenario uncertainty increases, and that by moving from a global to a regional scale the model and internal variability uncertainty can substantially increase. They also show that the European region has particularly strong internal variability (in this case in air temperature).

When we move to the climate impacts arena we add other aspects of uncertainty arising from, and propagating through, the downscaled models. Practicalities limit our ability to at best span aspects of the uncertainty with a limited number of simulations. Such an approach is an important first step and allows us to explore the system's response to the range of different drivers both qualitatively and quantitatively. However, the usefulness of the results as 'forecasts of future conditions' is questionable, as discussed by Skogen et al. (2011).

The opening question for explorations of climate change impacts tends to be 'how might anthropogenic climate change impact this process in the future?' An issue that immediately arises is that the forecast horizon required for the answer to be relevant, to policy decisions being considered now, is generally much shorter than that required to give a clear answer; i.e. the policy relevant time scales more closely match those of the natural variability than the longer term trends. For example, the planning cycle for MSFD is 6-years, so only a projection of many such cycles ahead will give a clear climate change signal against the background of natural variability. This is especially the case in regions, such as the North Atlantic, where natural variability arising from (e.g.) the position of the storm track and atmospheric processes such as blocking are so important. Moreover processes that are themselves non-linearly dependent on this natural variability, such as aspects of ecosystem function, are likely to exacerbate this issue through an exaggerated sensitivity to the details of the variability (e.g. through mixed layer depths). This mismatch between the time scales on which we can make clear statements on climate change, and the time scales over which decisions need to be made is a grand challenge in climate change impacts work. A possible mitigating effect is that ecosystems can act as integrators of their environmental conditions and so improve signal-to-noise ratios over their forcing, allowing for the detection of weaker climate change signals (Taylor et al., 2002). Hence it is more appropriate to re-frame the question so that climate change and variability are on a more equal footing, and ask: 'what is the range of possible impacts on this process, given present day statistics of variability and how they might change into the future?'.

An appropriate forecast horizon for EURO-BASIN is out to 2040, since this is most relevant for the issues of ecosystem function and their relation to (e.g.) fisheries and climate change mitigation policy. On this basis it is appropriate to use transient simulations here, which run continuously from the present to the future, rather than the 'time-slice' approach that is common in many downscaling type simulations (e.g. (Holt et al., 2012a)).

The forcing we consider must, therefore, treat the atmospheric dynamics and consequent natural variability as accurately as possible, and the analysis needs to explicitly capture the modes of response of the system. For example, inadequacies in the representation of the North Atlantic storm tracks (being too far south) in the AR4 class have previously been identified (Lowe et al., 2009), and whether this is rectified in the CMIP5 models needs to be critically examined. Such biases can have serious consequences when exploring the impact of climate change on the higher trophic levels of the ecosystem (Lehodey et al., 2012; Stock et al., 2011). A particular consideration for this study, is that the phase of the variability in AOGCM forced simulations is not constrained by observations, so the longer period modes (e.g. the Atlantic Multi Decadal Oscillation (AMDO); and Atlantic Meridional Mode; see Grossmann and Klotzbach, 2009) almost certainly will not be in the appropriate phase for a 2040 projection and the forecast horizon is not sufficient for these to average out in the statistics. The decadal climate prediction models used in CMIP5 (Taylor et al., 2012), whereby the climate model is initialised from present day observations, have the potential to address this. Recent investigations of the ensemble of these models suggests that they have some skill in retaining the

AMDO, with correlations at around the 90% significant level out to 9 years lead time (Kim et al., 2012), but beyond this scenario forcing becomes increasingly important (Branstator and Teng, 2012).

For EURO-BASIN, we adopt two approaches. First, the conventional approach and conduct a series of simulations forced by a small number of free-running CMIP5 AOGCM simulations, accepting that the phase of variability will not be coincident with reality; the simulations will be long enough to average out some of this (e.g. the North Atlantic Oscillation). The second approach also uses the CMIP5 outputs, but aims to correct the biases by perturbing a reanalysis based hindcast forcing set (DFS5; an update on Brodeau et al., 2010). The DFS5 atmospheric data is decomposed into realistic weather regimes, and analogs of these are defined in the AOGCM simulations of the present-day period. The evolution of these analogs is then statistically followed in future scenario IPCC simulations, and a forcing data for future simulations is constructed with these time evolutions, using the realistic weather regime previously defined (Cassou et al., 2011; Minvielle et al., 2011). Hence, the realism of the spatial structure of the future forcing is maintained and the evolution of the future forcing is given by statistics from the IPCC runs. Moreover, there is continuity and consistency between the (realistic) hindcast and forecast forcing.

Concluding remarks: integrating the EURO-BASIN models

EURO-BASIN is focused on creating predictive understanding of key species and the emergent ecosystem and biogeochemical features of the North Atlantic basin in order to further the abilities to understand, predict and contribute to the development and implementations of the ecosystem approach to resource management.

In order to link ecosystems and key species to carbon fluxes EURO-BASIN follows a trophic cascade framework, quantifying the flow of mass and elements between key species and groups, along with a size spectrum approach to establish and quantify the links between these trophic levels and assess the implications of changes in the players on the flux of carbon. To deliver this we draw on the state of the art in numerical modelling of the North Atlantic: high resolution ocean physics, biogeochemical models

of differing complexity, and a range of approaches to modelling mid and higher trophic levels are employed. Fig. 14 illustrates how the various modelling tools for assessing ecosystem characteristics discussed in this paper relate to each other and the stressors influencing the trophic cascade from primary producers to top predators. How this will proceed in practice in EURO-BASIN can be summarised as follows:

1. **Physics Biogeochemistry Coupler:** The three biogeochemical models (ERSEM, MEDUSA, PISCES) have been coupled with NEMO. There are three configuration of NEMO in use in EURO-BASIN;

- (i) 1/4°N Atlantic Basin: ERSEM, PISCES
- (ii) 1/4° Global Ocean: Medusa
- (iii) 1/12° NN Atlantic model (with shelf seas processes): ERSEM

The 1/4° domains are used for the regional hindcast, climate forced and re-analysis forced simulations, climate-scenario forced simulations, top down control perturbation experiments and a fully coupled end to end ecosystem model. The 1/12 model is for use in assessing the sensitivity of ecosystem response to key processes relating to mesoscale physics, shelf seas physics and spatial scale.

2. **MTL model coupling 1 way:** The suite of MTL models (MTL; APECOSM and the IBM) will be coupled off-line to the ensemble averages of the planktonic ecosystem states from the LTL reanalysis and future climate simulations (point 1).
3. **ERSEM–IBM coupler:** 2 way coupling of ERSEM with the Calanus IBM.
4. **PISCES–APECOSM coupler:** 2 way coupling of PISCES with the APECOSM.
5. **Parameterisation Convection IBM:** The Convection IBM model is being developed to explore the impact of deep convection on phytoplankton growth. The goal is to inform the parameterisation of these processes in the Eularian frameworks of the biogeochemical models.

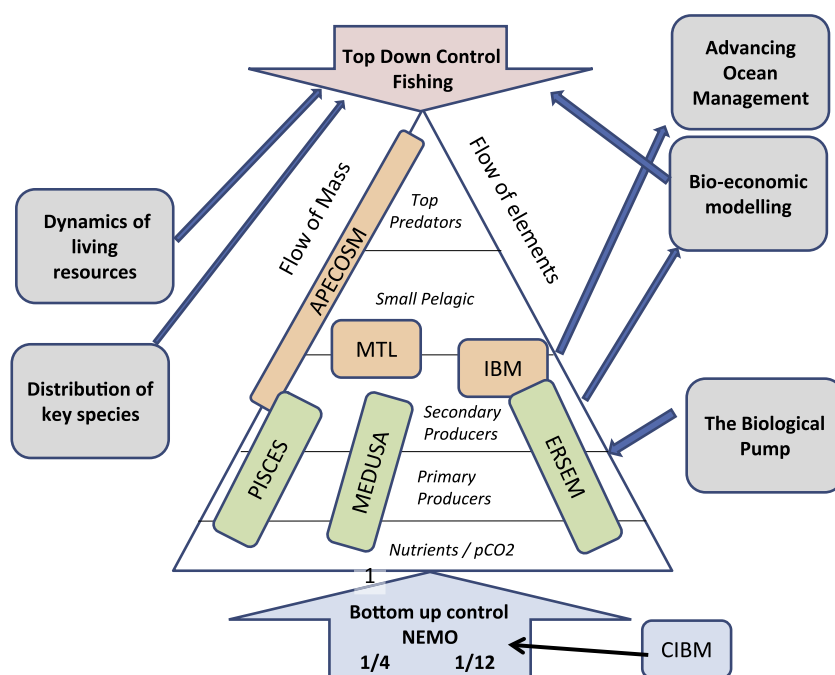


Fig. 14. Schematic diagram of the relationship between the EURO-BASIN models.

6. **Parameterisations of C export:** An analysis of existing algorithms for particle flux and based on historic observations and fieldwork is being undertaken (Sanders et al., this volume). Based on the recommendations from this work, parameterisations of particle flux will be amended and tested in the LTL models as appropriate.
7. **Habitats and estimates of top down control:** To assess the sensitivity of biogeochemical cycles to changes in grazing pressure, we will draw on information on habitats predation rates from other components in EURO-BASIN to design sensitivity experiments. Specifically, the development of habitat models will provide information for the validation of modelled biogeography, and estimates of herring, blue whiting and mackerel predation on LTL to help parameterise sensitivity experiment to top down control on biogeochemical cycles.
8. **Model outputs to drive economic and management models:** The integrative modelling will provide model outputs for facilitate other activities in EURO-BASIN, specifically
 - (i) MTL biomass estimates to drive tuna models.
 - (ii) LTL biomass estimates to drive herring, blue whiting and mackerel models.
 - (iii) Primary production to drive bioclimatic envelope models of fish.
 - (iv) Carbon budgets to estimating the economic value of the N Atlantic C pump.
 - (v) Hydrodynamic and biogeochemical information to drive the models underpinning the comparative analysis of foodweb structure.
 - (vi) LTL biomass estimates for the integrative analysis of past and future ecosystem change, using Artificial neural networks.
 - (vii) Habitat information for advancing fisheries management.

Hence, these tools will be used both singly and in combination to assess the emergent properties of the ecosystems, to create metrics for the prediction of future states and to contribute to the assessment and implementation of an ecosystem approach for the management of exploited resources. Full details of the on-going Basin-scale Integrative Modelling work in EURO-BASIN and the results as they emerge can be found at <http://www.EURO-BASIN.eu/>.

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